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Facilitation of *Agave potatorum*: An ecological approach for assisted population recovery

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ABSTRACT

Extraction of *Agave potatorum* from forests for mescal production is a main cause of its populations' decline and extinction in central Mexico. Sustainable harvest of agaves and populations' recovery actions are needed for protecting this and other agave species similarly threatened. Our study aimed to identify mechanisms determining seedling establishment and sapling plants growth of *A. potatorum* in order to generate information helpful for enhancing populations' growing and reforestation strategies. We hypothesized that (1) *A. potatorum* plants are spatially associated, probably species-specific, to shrub species, the frequency of facilitation being higher in the earlier stages of life cycle, varying among sites under different stress conditions, (2) germination and seedling survival are higher beneath nurse plants canopy compared with open areas, seeds and plants from a particular site performing better in the original conditions than in others, (3) nurse plants have a positive effect in the net balance of the growth rate of *A. potatorum* despite the negative effects of shade on carbon gain. We studied the association of *A. potatorum* with shrub and tree species by analysing their distribution patterns in two sites with contrasting environments (one relatively more xeric than the other). In these site we conducted experiments for testing seedling establishment and growth of agaves. Reciprocal transplanting experiments tested seed germination and seedling survival of agaves in open areas and beneath nurse plants. Two-years-old saplings were planted in open areas and beneath nurse plants to analyse their relative growth rate. We found a significant association of both young and adult plants to nurse plants, some of them being markedly specific. Germination and survival were higher under nurse plants, we also found negative effects of shade in carbon gain, but growth was higher there than in open spaces. We suggest that protection against solar radiation is a main factor influencing the association. Provenance of seeds was significant for germination success and early establishment. Nurse plants are crucial for the establishment of *A. potatorum*; however, several species may play the role of nurse plants and these may be different among sites. Therefore, rapid identification of nurse plant species in different vegetation types would allow agile actions for successful reforestation. Manual dispersion of seeds beneath canopies of shrubs that are high quality nurse plants, as well as producing sapling agaves in nurseries and transplanting them after two years associated to nurse plants are recommendable techniques for populations' recovery.

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1. Introduction

Facilitation is a crucial positive plant–plant interaction for survival, growth, and general performance of a number of plant species (Brooker et al., 2008; Callaway, 1995). It is also fundamental for structuring biotic communities and maintaining their diversity (Armas and Pugnaire, 2005; Michalet et al., 2006; Miriti, 2007; Valiente-Banuet and Verdú, 2007; Verdú and Valiente-Banuet, 2008), consequently, facilitation may be a key factor for species management and forest recovery plans.

Nurse plants provide facilitation beneath their canopies, where beneficiary plants find favourable environments for seedling establishment, survival, growth and reproductive output compared with open areas (Baumeister and Callaway, 2006; Callaway, 1995; Filazzola and Lortie, 2014). Canopy shade decreases solar radiation, buffers extreme temperatures, and reduces evapotranspiration (Gómez-Aparicio et al., 2005a–c; Valiente-Banuet and Ezcurra, 1991). Nurse plants may also increase available organic matter, soil nutrients, and water availability (Callaway, 1995; Dawson, 1993; Gómez-Aparicio et al., 2005b; Pugnaire et al., 2004, 1996), and

may influence indirect interactions with other plant species, herbivores, mycorrhizal fungi, pollinators and dispersers (Callaway, 1995; van der Heijden and Horton, 2009; van der Putten, 2009). This plant–plant interaction is dynamic and may have negative effects (Holmgren et al., 1997), such as reduction of photosynthetic active radiation (PAR), competence for water and resources, and interception of rain, among others. The outcome of this interaction depends on the balance between costs and benefits on vital functions of the interacting plants and the effects of other factors (Baumeister and Callaway, 2006). Such balance can be mediated by the environmental conditions and resources availability and could change throughout the life cycle (Miriti, 2006; Valiente-Banuet and Verdú, 2008). In addition, it may involve phenotypic plasticity (Liancourt and Tielbörger, 2011) influencing offspring development patterns that may give rise to specific associations (Callaway, 1998), and changes in the sign and intensity of the interactions along stress gradients (Bertness and Callaway, 1994; Callaway and Walker, 1997).

The importance of facilitation to explain the dynamics of populations and communities has led to consider this interaction as a key factor for vegetation restoration and the recovery of declining populations (Brooker et al., 2008; Castro et al., 2004; Cortina et al., 2011; Gómez-Aparicio, 2009; Gómez-Aparicio et al., 2004; Maestre et al., 2001; Padilla and Pugnaire, 2006). This is the case for several species of Agave, a genus widely distributed in México where these plants also bear their highest diversity (Gentry, 1982). Populations of more than 150 agave species have been used by Mexican peoples as food, construction, cords, clothing, firewood, and other purposes (Colunga-GarcíaMarín et al., 2007), but extraction of agave products from forests have affected their populations. Agaves are abundant in several vegetation types throughout México (Gentry, 1982) and at least 53 species have been used by local cultures for production of distilled beverages called 'mescal' (Colunga-GarcíaMarín et al., 2007; Delgado-Lemus et al., 2014b; Torres et al., 2015). Most species used with this purpose are wild plants harvested from forests, just before sexual reproduction and, consequently, agave populations used have been severely damaged. Some species, among them Agave potatorum Zucc. are now considered highly endangered because of their extraction for mescal production (Casas et al., 2008; Delgado-Lemus et al., 2014b). In the case of A. potatorum, it has been documented that in some traditional rural communities, people may extract 54–87% of all reproductive individual plants per year in their territories, but populations closer to the village are even more intensively extracted, becoming extinct in some localities (Delgado-Lemus et al., 2014a).

For maintenance of A. potatorum populations, it is recognized the need to assist population recovery, by enhancing seedling recruitment in wild populations in situ, as well as by producing and maintaining plants in nurseries, and then planting young plants in forests and traditional agroforestry systems (Delgado-Lemus et al., 2014a,b; Moreno-Calles and Casas, 2010; Torres et al., 2015). Such management strategies can be alternative models to the intensive monocultures of Agave angustifolia Haw. and Agave tequilana Weber, which have generated problems such as loss of genetic diversity and forest cover, soil erosion and contamination because of the use of agrochemicals, and the high cost of maintaining intensive systems (Bowen and Valenzuela Zapata, 2009; Martínez et al., 2007; Sánchez, 2005). Therefore, information about factors and mechanisms related to the establishment of agave seedlings and saplings in order to develop appropriate techniques for their recovery and sustainable use of their populations is urgently needed.

Studies of seedling establishment in agave species have documented to occur similarly to other succulent plant species, with low recruitment rates associated to events of high rainfall and associated to nurse plants. These are for instance the cases of Agave deserti Engelm. (Nobel, 1992), Agave macroacantha Zucc., Agave karwinskii Zucc., Agave marmorata Roezl, Agave peacocki Croucher, and Agave salmiana Otto ex Salm-Dyck (Arizaga and Ezcurra, 2002; Valiente-Banuet and Verdú, 2008). Therefore, developing experiences of assisted populations' recovery with A. potatorum may be useful for several Agave species.

We assumed that if A. potatorum is a facilitation beneficiary: (1) seedlings, sapling and adult plants of A. potatorum are spatially associated with shrub species; their distribution around the shrubs being not at random but according to the shrub shade projection, and the frequency of facilitation being higher in sites with higher environmental stress; (2) germination and survival is higher under shrub canopies compared with open areas and could be different between shrub species (differences in nursing quality); similarly, seed provenance is also important for germination and seedling performance in different environments; and (3) nurse plants have a positive effect in the net balance of the growth rate of A. potatorum plants, even though the negative effects of shade on carbon gain and leaf production. For testing these hypotheses, we identified the association and possible specificity in seed germination, seedling establishment and growth in sites with relatively more xeric and mesic environments, respectively, considering that the identity of nurse plant species with significant association is crucial for designing populations' recovery. We expected to identify the mechanisms of facilitation to A. potatorum in order to determine bases to develop methods for populations' recovery for this and other agave species influenced by facilitation.

2. Material and methods

2.1. Study area

Our study was carried out responding to a demand of information to improve results of actions for reforesting A. potatorum by the community of San Luis Atolotitlán Puebla, in the Tehuacán Valley, central Mexico. Local people have been carrying out actions in this direction since 2004, but their success is hindered by the high mortality of sapling agaves planted in the forest (Casas et al., 2008; Torres et al., 2013).

Rainfall in the study area is highly variable, having ranged from 187 to 845 mm per year in the last 50 years (Quintas, 2000). One of the sites studied belongs to the territory of the community of San Francisco Xochiltepec (ahead called mesic site), located at 97°25′4.85″W, 18°13′6.28″N, and elevation of 2100 m, in a slope south-eastern oriented, with soils 20–30 cm deep, derived from calcareous rocks (Appendix A). This site has relatively more mesic environmental conditions than the second site described below; vegetation is scrub forest dominated by Euphorbia rossiana Pax, with a shrubby-arboreal stratum up to 1.7 m in height. The canopies cover more than 90% of the total surface, leaving small open areas less than 1 m² each. In this site, adult individuals of A. potatorum average 57 ± 10 cm in height, with a canopy diameter averaging 77 ± 15 cm, generally acaulescent, with dark green leaves.

The other site is located in the hill called Machiche, in the territory of the village of San Luis Atolotitlán (ahead called xeric site), 2 km apart from the mesic site. This site is located at 97°25′30.77″W, 18°12′7.39″N, and elevation of 2300 m, in a slope south-eastern oriented. Vegetation is thorn-scrub forest dominated by Dasylirion serratifolium Baker and Gochnatia hypoleuca A. Gray. It is distributed in patches of less than 1 m² each, with shrubby components averaging 60 cm in height. The total vegetation canopies cover 35% of the surface, the soils are 15 cm deep and are derived from calcareous rocks (Appendix A). In this site the

environment is relatively more xeric than in the mesic site, with lower temperatures, higher relative humidity, higher albedo caused by calcareous rocks emerging in open areas and stronger wind incidence (Appendix A). Adult individuals of *A. potatorum* have on average 33 ± 7 cm in height and 41 ± 7 cm in diameter, most frequently being caulescent, with glaucous or reddish green leaves. Nearly 30% of plant species composing the vegetation are shared among the studied sites.

2.2. Species description

A. potatorum produces relatively small rosettes, it is semelparous and its effective propagation is only through sexual means (Gentry, 1982), which occurs 10–12 years after germination. The blooming season is from September to December and it is pollinated by bats of the genus *Leptonycteris* (Estrella-Ruiz, 2008). A total of 2000–9500 seeds are produced per individual plant (Torres et al., 2015), which are dispersed by the wind from January to April. Seed germination occurs during the rainy season between June and September. *A. potatorum* is endemic to the states of Puebla and Oaxaca, central Mexico ranging at elevations between 1300 and 2400 m. It grows in tropical deciduous forest, xeric shrubland and their transitions to *Quercus* forest on thin soils derived from calcareous rocks (García-Mendoza, 2011). It may be morphologically variable according to features of local environment, a fact recognized and used by people to decide which places provide agaves for the best mescal quality.

2.3. Methods

2.3.1. Spatial distribution and association

In each site we established a 2500 m^2 plot where we estimated the total surface open areas, and recorded two diameters of the canopies of all perennial plants inside the plot (ahead referred to as micro-environments), in order to estimate the total surface of each micro-environment within the sampled area. All individuals of *A. potatorum* were recorded, indicating their height, if they were in open spaces or associated to other plant species (beneath their canopies) and their azimuth orientation with respect to the associated plants (North from 315° to 360° and 0° to 45°, East from 45° to 135°, South from 135° to 225°, West from 225° to 315°). In order to detect ontogenic shifts in the association patterns, the agaves recorded were classified into two groups, one comprising seedlings and sapling plants (less than 35 cm in the mesic site and less than 20 cm in the xeric site, respectively), and the other including nearly adult and adult plants (35–80 cm in height in the mesic site and 20–54 cm in the xeric site, respectively).

In order to determine whether the frequency of facilitation differed among mesic and xeric sites in shared microenvironments, we estimated the relative intensity index RII (Armas et al., 2004), calculated as RII = (*Pnurse* − *Popen*)/(*Pnurse* + *Popen*), where *Pnurse* was the number of agave plants under the canopy of a plant and *Popen* the number of agave plants recorded in open spaces (Armas et al., 2011; Soliveres et al., 2012).

2.3.2. Seed germination and seedling survival

Preliminary experiments of seed germination were conducted in order to evaluate the germination rates of seeds from the two study sites at 25 °C and neutral photoperiod (12 h light/darkness) in a growth chamber (Percival Scientific I-35 LL, Boone, Iowa). Five replicates of 50 seeds each were placed in petri dishes with 1% agar. Before the experiment, seeds were disinfected during 15 min in a solution of 70% NaClO. Germination was recorded every 24 h for 15 days; seeds were considered to have germinated when radicle protrusion was observed.

In order to compare how microenvironments and provenance site of seeds influence the establishment of agaves, reciprocal transplanting experiments were conducted in both study sites; seeds from the two sites were sowed in open spaces and beneath canopies of four plant species. To evaluate the impact of predation we included treatments with and without dispositive of exclusion of predators in open areas and beneath canopies of four shrubs species. The species selected were *E. rossiana*, *Rhus chondroloma* Standl., *Pterostemon rotundifolius* Ramirez, *Wimmeria microphylla* Radlk. in the mesic site, and *G. hypoleuca*, *P. rotundifolius*; *Amelanchier denticulate* (Kunth) K. Koch, and *Calliandropsis nervosus* (Britton & Rose) H.M. Hern. & P. Guinet in the xeric site (a description of the conditions under their canopies is provided in Appendix A). These species were selected considering the surface covered by their canopies, in order to ensure the availability of enough area for the experimental treatments and repetitions, as well as the association with *A. potatorum*.

Experimental treatments included five replicates, each one with 50 seeds. Seed predators' exclusion dispositives were designed to exclude birds, rodents and not flying insects; these were 25 cm diameter metallic net cages, and using the resin "tangle foot" at the basis of the cage. Treatments without exclusion were labelled with circles 25 cm diameter made of stones of less than 5 cm in height.

We recorded seed germination by observing their emergence every two days for two weeks and then seedling survival and new emergence every 30 days during one year. We considered that the total percentage of seedling emergence was the maximum number of seedlings recorded until 99 days after starting the experiments.

The seeds for all experiments were collected from reproductive plants in each site from at least five agave plants. Seeds of each site were mixed and stored in paper bags in darkness at 20.6 ± 0.05 °C and 57% of relative humidity.

2.3.3. Carbon gain

We measured the nocturnal increasing of titratable acidity of malic acid in foliar tissue as indicator of the amount of CO_2 fixed during the night (Nobel, 1988). We collected 10 tissue samples (4.5 cm^{-2} each) of the youngest leaf north oriented from individuals of 20–40 cm height established in the microenvironments used for testing establishment; the only exception was *Amelanchier denticulata* in the xeric site where it was scarce. Instead, we used the microenvironment of *D. serratifolium*.

Samples were collected at dawn and at dusk and immediately were conserved in liquid nitrogen. The samples were grounded, diluted in 30 ml of distilled water and titrated with NaOH 0.01 N up to pH 7. The increase rate of titratable acidity was calculated as the difference of ml of NaOH used in samples collected at dusk, with respect to those collected at dawn, multiplied for the molarity of the solution (Nobel, 1988).

2.3.4. Growth

We transplanted into the study sites two years old sapling agaves with 10.3 ± 0.2 leaves, which were produced in a nursery at the community of San Luis Atolotitlán. In each site we transplanted 15 agaves in each microenvironment used in the experiments (Appendix A). We measured height, two perpendicular diameters and the number of leaves of each agave planted at the beginning and at the end of the experiment that lasted 337 days.

The relative growth rate (ahead RGR) was estimated by assessing the volume of the individual plants since rosettes grow in both height and diameter. This method avoided destructive measurement of biomass. For this purpose we used the formula: $(\ln Vt_2 - \ln Vt_1)/t_2 - t_1$ (Gómez-Aparicio et al., 2005b), in which Vt_1 was the volume at the beginning of the experiment and Vt_2

was the volume after 337 days. In addition, the total number, the production and mortality of leaves was also considered. The volume of plants was estimated using the formula: $V = 4\pi/3ab^2$, in which a was the height and b was the average of the perpendicular radius.

2.4. Data analyses

2.4.1. Spatial distribution and association

In order to identify whether or not *A. potatorum* plants at different stages of their life cycle were associated to specific microenvironments we performed Chi-square goodness of fit tests for seedlings–sapling and adult plants stages of *A. potatorum* per mesic and xeric site. The expected number of agaves associated to each environment was estimated based on the probability that one *A. potatorum* plant was found at random in a microenvironment, which was estimated by the proportion of the total surface occupied by each microenvironment. Microenvironments with expected values lower than 5 were grouped (Asteraceae, Fabaceae and others) in order to meet the criteria of Chi-square test (Sheskin, 2004). To identify which microenvironments or cells had a higher contribution to the significant differences in Chi-square tests, we calculated the standardized residuals as $R = (O - E)/\sqrt{E}$, where O was the observed and E the expected agave individuals. For this purpose, we considered that cells with absolute residual values $\geqslant 1.96$ at $\alpha \leqslant 0.05$ were significant microenvironments (Sheskin, 2004). We in addition assumed that positive values indicated that *A. potatorum* was specifically associated to that microenvironment, whereas negative values indicated that *A. potatorum* was not associated to that microenvironment. The data analyses were performed through STATISTICA 6 (StatSoft-Inc., 2003).

For determining whether or not the orientation of *A. potatorum* plants with respect to the closest plant shrub was placed at random in each site, we conducted Chi-square goodness of fit tests and checked the standardized residuals to identify which azimuth orientation had a higher contribution to *A. potatorum* distribution orientation. The expected values were calculated dividing the total number of *A. potatotum* plants recorded in each of the four azimuth orientations.

In order to determine if microenvironment association frequency differed among sites we compared the interaction intensity index RII of shared microenvironments between sites through a Wilcoxon Signed-Rank Test (Sheskin, 2004).

2.4.2. Germination and seedling survival

The effect of microenvironment and exclusion of predators on seed germination was analysed by site using factorial ANOVAs and Tukey multiple range tests, previously testing the normality of data. These analyses were conducted through STATISTICA 6 (StatSoft-Inc., 2003).

The effect of seed provenance (mesic or xeric site), micro-environment and seed predators' exclusion on survival rate (proportion of seedlings alive per month) was evaluated through deviance analyses using GLM (Crawley, 1993) by site. In the model, the proportion of surviving seedlings was the dependent variable and time was the independent one. The two sites of seeds provenance, the five micro-environments treatments with and without exclusion of seed predators were all categorical variables. We used the binomial error and a logistic link function as indicated for proportional dependent variables. For this error type the deviance (equivalent to variance in a model with normal type error) explained by independent variables can be considered to be an approximated Chi-square value (Crawley, 1993). The proportion of seedlings survival after t days was given by the model:

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

In this model y is the proportion of seedlings survival, a is the intercept or the starting of the seedling survivorship decreasing, b is a coefficient indicating the starting survival rate, c is a coefficient indicating how the survival rate decreases. The effect of seeds provenance site, the micro-environment and the seed predators' exclusion on seedling survival was evaluated as the deviance explained by the interaction of each factor or both with the linear (t) and quadratic time (t^2). The deviance explained by each independent variable was calculated based on values of Chi-square at $\alpha < 0.05$ (Crawley, 1993). Statistical analyses were conducted using software GLIM version 3.77 (Royal-Statistical-Society, 1985). In cases in which a term was not significant it was removed from the model.

2.4.3. Carbon gain and growth

The differences in RGR, the total number of leaves per plant, the leaf production and mortality, and titratable acidity in agave plants associated to five microenvironments in each site, were tested through factorial one-way ANOVAs by variable and per site. Tukey multiple range tests were performed for significant differences. Non-normal variables were analysed by Kruskal–Wallis tests (Sheskin, 2004). All these analyses were conducted with STATISTICA 6 (StatSoft-Inc., 2003).

3. Results

3.1. Spatial distribution

3.1.1. Association

In the mesic site we recorded 226 individual plants of *A. potatorum,* only 4% of them distributed in open spaces, 6% associated to dead shrubs, and 90% associated to 22 (from a total of 76) species of shrubs and trees recorded in the site. Seedlings and sapling plants of *A. potatorum* were distributed in a non-random pattern ($X^2 = 39.72$, $df = 9$, $p < 0.001$), similarly as adult plants ($X^2 = 21.445$, $df = 9$, $p = 0.011$). Seedlings and sapling agaves were particularly more abundant than expected beneath the canopy of *E. rossiana* (Table 1) and less than expected under the canopy of *Krameria cytisoides* (Table 1). Adult plants were less abundant than expected also under canopy of *K. cytisoides* and in open areas (Table 1).

In the xeric site we recorded a total of 234 individual plants of *A. potatorum,* 19.66% of them distributed in open areas, 2.14% associated to dead shrubs and 78.2% associated to 21 (from a total of 59) species of shrubs recorded. Seedlings and saplings of *A. potatorum* were not distributed at random ($X^2 = 98.29$, $df = 4$, $p < 0.001$), similarly as adult plants were not ($X^2 = 224.442$, $df = 4$, $p < 0.001$) (Table 1). Both seedling–sapling and adult agave plant categories were significantly associated to *G. hypoleuca*. Agave plants from both categories analysed were significantly less abundant than expected in open areas (Table 1).

3.1.2. Orientation in relation to the nurse plant

In all our records, *A. potatorum* plants were significantly oriented towards north and west (in the mesic site: $X^2 = 30.531$, $df = 3$, $p = < 0.001$; in the xeric site: $X^2 = 46.895$, $df = 3$, $p = < 0.001$) (Fig. 1).

3.1.3. Frequency of facilitation between sites

The frequency of facilitation in microenvironments shared in the two sites studied were not significantly different ($Z = 1.1976$, $df = 18$, $p = 0.231$) (Fig. 2, Appendix B).

Table 1
Percentage of area covered by canopies of perennial plant species and open spaces in the mesic and xeric sites. Number of individual plants of *Agave potatorum* observed, number expected and standardized residual values of the association with seedlings, sapling and adult plants (* absolute values of standardized residuals ⩾1.96 are significant at $p < 0.05$ by Chi-square test).

Species	Area (%)	Agaves observed	Agaves expected	Standardized residuals
Mesic site				
Seedlings and sapling plants				
Bursera sp.	6.322	6	8.471	−0.849
Euphorbia rossiana	14.129	41	18.932	5.072*
Krameria cytisoides	6.541	1	8.765	−2.623*
Pterostemon rotundifolius	8.211	14	11.003	0.903
Rhus chondroloma	8.429	7	11.295	−1.278
Wimmeria pubescens	10.201	13	13.669	−0.181
Open spaces	10.037	7	13.450	−1.759
Asteraceae (9 species)[a]	9.645	12	12.924	−0.257
Fabaceae (10 species)[a]	13.426	19	17.990	0.238
Other 51 species and dead shrubs[a]	13.059	14	17.499	−0.837
Adult plants				
Bursera sp.	6.322	3	5.816	−1.168
Euphorbia rossiana	14.129	17	12.998	1.110
Krameria cytisoides	6.541	1	6.018	−2.045*
Pterostemon rotundifolius	8.211	11	7.554	1.254
Rhus chondroloma	8.429	8	7.755	0.088
Wimmeria pubescens	10.201	15	9.385	1.833
Open spaces	10.037	2	9.234	−2.381*
Asteraceae (9 species)[a]	9.645	6	8.873	−0.965
Fabaceae (10 species)[a]	13.426	11	12.352	−0.385
Other 51 species and dead shrubs[a]	13.059	18	12.014	1.727
Xeric site				
Seedlings and sapling plants				
Gochnatia hypoleuca	11.2	32	12.6	5.448*
Open spaces	64.7	25	73.1	−5.629*
Asteraceae (15 species)[a]	4.4	15	5.0	4.463*
Fabaceae (12 species)[a]	4.3	11	4.8	2.799*
Other 31 species and dead shrubs[a]	15.4	30	17.4	3.028*
Adult plants				
Gochnatia hypoleuca	11.2	48	13.5	9.372*
Open spaces	64.7	21	78.3	−6.477*
Asteraceae (15 species)[a]	4.4	13	5.4	3.296*
Fabaceae (12 species)[a]	4.3	16	5.2	4.750*
Other 31 species and dead shrubs[a]	15.4	23	18.6	7.825*

[a] In these cases species were grouped because individually almost all had less than 1 expected values.

3.2. Seed germination and seedling emergence

In laboratory at 25 °C and neutral photoperiod, the final percentage of seeds germination from the xeric site was different ($F = 11.902$, $df = 1$, $p = 0.009$). Germination of seeds from the xeric site was on average $92.8 \pm 1.4\%$ and that from the mesic site $82.8 \pm 2.7\%$.

In the mesic site, the final percentage of seedling emergence was influenced by the microenvironment ($F = 6.135$, $df = 4$, $p < 0.001$) and the exclusion from predators ($F = 37.433$, $df = 1$, $p < 0.001$). The highest percentages of seedling emergence were recorded under the canopy of *R. chondroloma* and the predation exclusion treatments, whereas the lowest percentages were recorded in open areas (Table 2). The site of seed provenance was no significant ($F = 2.071$, $df = 1$, $p = 0.154$), but it was significant in interaction with microenvironment ($F = 3.281$, $df = 4$, $p = 0.015$), the lowest emergence percentages recorded for seeds of the mesic site was in open areas, whereas for seeds of the xeric site the lowest emergence percentages were recorded under the canopy of *E. rossiana* and open areas (Table 2).

In the xeric site there were no significant differences in seedling emergence neither among microenvironments ($F = 1.393$, $df = 4$, $p = 0.242$), nor among treatments excluding or not predators ($F = 2.566$, $df = 1$, $p = 0.113$) (Table 2). But the site provenance of seeds was a significant factor ($F = 6.342$, $df = 1$, $p = 0.014$), seedling emergence was higher for seeds from the xeric site. The interaction of seed provenance and microenvironment was also significant ($F = 7.16$, $df = 4$, $p < 0.001$). The seedling emergence from seeds of the xeric site was higher under the canopies of *P. rotundifolius*, *A. denticulata* and *G. hypoleuca*, whereas that of the mesic site was higher in open areas (Table 2).

3.3. Seedling survival

After 411 days of starting the experiment, in the mesic site only 15 seedlings survived. Exclusion against predators was the main factor explaining 26% of the deviance (Fig. 3, Table 3). The microenvironment explained 8%, and the seeds provenance explained 2% (14 surviving seedlings were from seeds of the xeric site). Seedlings from seeds of the two sites had the highest survival rate in treatments with predators' exclusion beneath the canopies of *R. chondroloma*, *P. rotundifolius* and *E. rossiana*, whereas the lowest rate occurred in open areas. Only one seedling survived in treatments without exclusion to the end of the experiment under the *R. chondroloma* (Fig. 3).

In the xeric site, eight seedlings remained alive in the treatments with exclusion of predators, explaining 11% of the survival
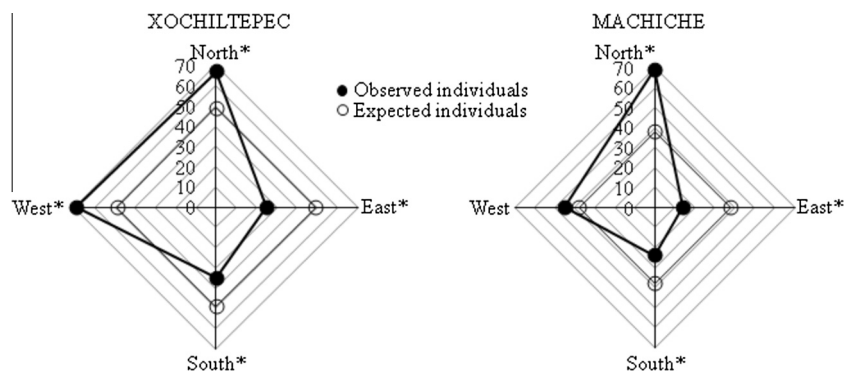

Fig. 1. Azimuth orientation of *Agave potatorum* individual plants with respect to the closest plant shrub in mesic and xeric sites. Azimuth orientations followed with an asterisk are significant at $p < 0.05$ (absolute values of standardized residuals ⩾1.96 by Chi-square test).
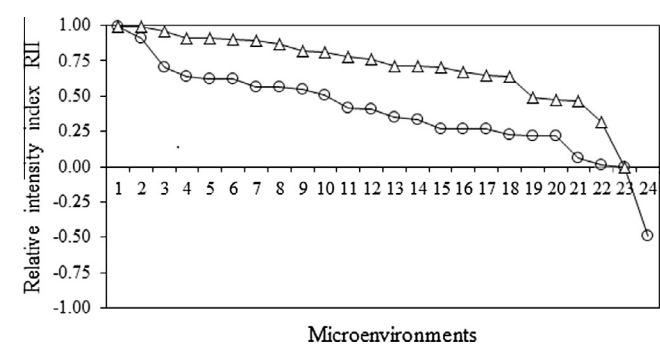
Fig. 2. Frequency of facilitation between sites (intensity of the interaction index RII) of *Agave potatorum* with shrubs shared between the mesic and xeric sites studied. Solid bars indicate interactions in the mesic site, empty bars indicate interactions in the xeric site.

deviance (Fig. 3, Table 3). The microenvironment explained 14% of the deviance, since six seedlings were beneath canopies of *C. nervosus*, *P. rotundifolius* y *G. hypoleuca,* mientras que dos se encontraban en los espacios abiertos. The site of provenance of seeds and its interaction with the microenvironment and exclusion of predators explained 23% of deviance. Five of eight seedlings surviving were from seeds of the mesic site, three were beneath the canopy of *P. rotundifolius* and two open areas, while the other three surviving seedlings were from seeds of the xeric site and were beneath the canopies of *G. hypoleuca* and *C. nervosus* (Fig. 3, Table 3).

In both sites time was significant (Table 3), indicating that the survival rate declined throughout time. Only in the xeric site slopes of curves that describe survival rates, measured through the quadratic time, varied significantly between some micro-environments with respect to the exclusion (Table 3, Appendix C), under the canopies of *C. nervosus* and *G. hypoleuca* without exclusion. The maximum mortality rates were reached more quickly than in open areas and than beneath the canopy of *P. rotundifolius* (Fig. 3, Appendix C).

3.4. Carbon gain

The average titratable acidity of *A. potatorum* in the mesic site was 66.51 ± 6.14 mmol H^+ m^{-2} and no significant differences were found between plants in open areas and those under shrub canopies ($H = 0.59$, $df = 4$, $p = 0.975$; Fig. 4).

In the xeric site the average titratable acidity was 62.22 ± 7.94 mmol H^+ m^{-2}. Plants in open spaces had values

significantly higher than those under shrub canopies ($H = 11.78$, $df = 4$, $p = 0.019$; Fig. 4).

3.5. Sapling agave plants growth

In the mesic site the RGR was positive in all treatments (Fig. 5), but significantly higher beneath shrub canopies compared with those agaves transplanted in open areas ($F = 11.80$, $df = 4$, 67, $p < 0.001$). The average number of leaves of sapling agaves after 337 days of transplanted was 9.04 ± 0.28, with no significant differences among microenvironments ($F = 0.92$, $df = 4$, 67, $p = 0.457$; Fig. 5). On average, the sapling agaves produced 3.67 ± 0.15 leaves during the experiment. The individuals transplanted under *E. rossiana* produced significantly less leaves ($H = 12.01$, $df = 4$, $p = 0.017$), while those transplanted in open spaces produced more leaves, similarly to the treatments beneath the canopies of *R. chondroloma*, *W. microphylla* and *P. rotundifolius* (Fig. 5). No significant differences were identified in leaf mortality among treatments ($H = 8.88$, $df = 4$, $p = 0.064$; Fig. 5).

In the xeric site, the RGR was negative in open areas, and it was significantly lower than growth of those agaves transplanted beneath the shrub canopies ($H = 31.118$, $df = 4$, $p < 0.001$). However, there were no differences between environments under canopies of shrub species (Fig. 5). The average number of leaves of the transplanted agaves by the end of the experiment was 8.10 ± 0.26, which was significantly lower in open areas ($F = 2.93$, $df = 4$, $p = 0.027$; Fig. 5). Average leaf production was 2.71 ± 0.14 per plant, which was significantly higher in open areas than under shrub canopies ($H = 10.69$, $df = 4$, $p = 0.030$; Fig. 5). However, agaves transplanted to open areas had significantly higher leaf mortality ($H = 26.52$, $df = 4$, $p < 0.001$) than agaves transplanted under shrub canopies; the lowest mortality was identified under *G. hypoleuca* (Fig. 5).

4. Discussion

Plants of *A. potatorum* were not distributed at random. In both sites, agaves were significantly associated to shrubs while scarce or absent in open areas, a pattern that suggests that facilitation is fundamental for the permanence and recovering of populations of this species. In addition, this result indicates that facilitation plays an important role in structuring the communities where this and other agave species occur (Arizaga and Ezcurra, 2002; Valiente-Banuet and Verdú, 2008). In the xeric site, the association to shrubs occurs in the states of seedling–sapling, as well as in adults, whereas in the mesic site the lowest number of *A. potatorum* individuals was identified in open areas but it was

Table 2

Seedling emergence (mean percentage ± standard error) at the end of the experiment. Treatments with seeds from mesic and xeric sites in open areas and beneath canopies of four plant species per site, with and without exclusion of predators. Means followed by different superscript letters are significantly different at $p < 0.05$ by factorial ANOVAs and Tukey multiple range tests.

| Microenvironment	Seeds from the mesic site		Seeds from the xeric site	
	With exclusion	Without exclusión	With exclusion	Without exclusión
Mesic site				
Open spaces	4.0 ± 1.5[abcde]	2.4 ± 0.9[cde]	7.600 ± 1.6[abcde]	4.800 ± 2.2[abcde]
Euphorbion rossiana	13.6 ± 3.3[abc]	2.8 ± 0.8[bcde]	8.800 ± 3.1[abcde]	0[e]
Pterostemon rotundifolus	10.4 ± 2.2[abcd]	2.8 ± 1.7[cde]	13.200 ± 4.4[abcd]	2.000 ± 2.0[de]
Rhus chondroloma	13.6 ± 4.7[abcd]	6.4 ± 1.7[abcde]	20.400 ± 4.7[a]	15.600 ± 6.0[abc]
Wimmeria microphylla	7.6 ± 2.8[abcde]	4.8 ± 2.1[abcde]	18.000 ± 4.1[ab]	7.600 ± 2.1[abcde]
Xeric site				
Open spaces	15.6 ± 3.8[a]	16.0 ± 5.0[a]	3.600 ± 1.5[ab]	2.400 ± 1.2[ab]
Gochnatia hypoleuca	5.6 ± 5.1[ab]	0.8 ± 0.8[ab]	12.800 ± 5.9[ab]	2.000 ± 0.9[ab]
Pterostemon rotundifolus	5.2 ± 4.7[ab]	0[b]	11.600 ± 4.6[ab]	12.000 ± 7.3[ab]
Amelanchier denticulata	1.2 ± 1.2[ab]	2.4 ± 2.4[ab]	9.200 ± 3.1[ab]	6.800 ± 2.9[ab]
Calliandropsis nervosus	3.6 ± 1.2[ab]	1.6 ± 0.9[ab]	5.200 ± 3.4[ab]	14.000 ± 7.3[ab]
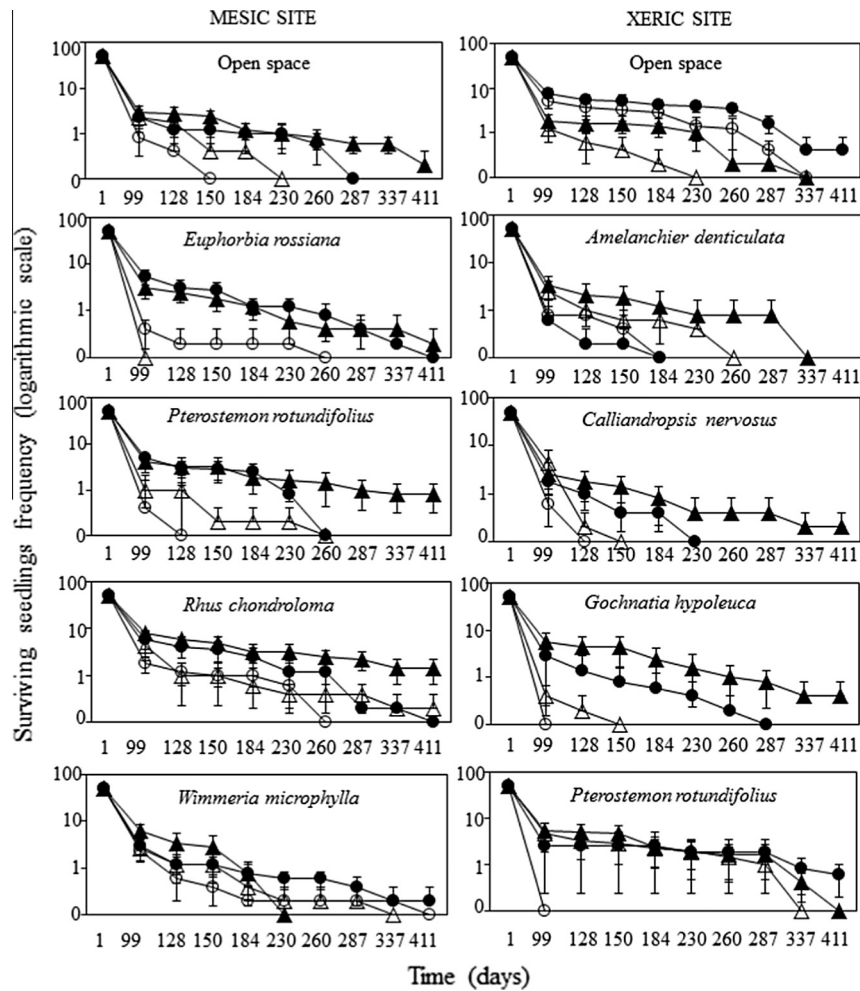
Fig. 3. Seedlings survival (means ± standard error) in open spaces and beneath canopies of four plants species with and without exclusion of predators in mesic and xeric site. Circles indicate seedlings originating from the mesic site seeds, triangles those from the xeric site seeds; solid symbols indicate treatments with exclusion, those empty indicate treatments without exclusion.

Table 3

Deviance analysis of the seedling survival in mesic and xeric sites, in open spaces and beneath canopies of four plants species with and without exclusion of predators.

Factor	Deviance (X^2)	df	r^2	p
Mesic site				
Seed provenance	5.900	1	0.019	0.015
Micro-environment	25.885	4	0.083	<0.001
Exclusion	79.99	1	0.258	<0.001
Micro-environment ∗ exclusion	11.947	4	0.038	0.018
Time	143.500	1	0.462	<0.001
Model	267.222	11	0.861	
Error	43.151	168	0.139	
Total	310.41	179		
Xeric site				
Micro-environment	49.540	4	0.144	<0.001
Exclusion	37.730	1	0.110	<0.001
Seed provenance ∗ micro-environment	62.870	5	0.183	<0.001
Micro-environment ∗ exclusion	15.492	4	0.045	0.004
Seed provenance ∗ micro-environment ∗ exclusion	18.356	5	0.053	0.003
Time	120.810	1	0.351	<0.001
Time ∗ micro-environment ∗ exclusion	17.51	9	0.051	0.041
Quadratic time	4.15	1	0.012	0.042
Model	326.458		0.948	
Error	17.799	149		
Total	344.26	179		

significant only for adult agaves, which suggests that although facilitation is important in both sites, there are differences among sites. Agave plants are mainly established at north and west orientation with respect to the nurse plants in both sites. This fact supports the suggestion that canopy shade is determinant of favourable conditions for establishment. It is important to consider that in the Tehuacán Valley, solar radiation is lower in the western side of the nurse plants throughout the day and in their northern side throughout the year. Such distribution pattern contrasts with that reported for some cacti species of the region, which although are generally associated to nurse plants, it has been recorded that their azimuth orientation is randomly distributed with respect to the nearest main stem of the shrubs (Valiente-Banuet et al., 1991). This pattern suggests that species like *A. potatorum* are more susceptible to damage by excessive solar radiation (Nobel, 1988) than species randomly oriented, reason why protection by shade is particularly important. We suggest that shade provided by nurse plants canopies is a main factor determining facilitation of *A. potatorum*, but other factors influencing in a nested hierarchical way should not be discarded (Baumeister and Callaway, 2006).

It has been proposed that the distribution associated to shrubs may be due to patterns of distribution of seeds caused by their differential dispersal (Suzán-Azpiri and Sosa, 2006). We consider that this factor influences indeed. Seeds may be accumulated and even germinate in open areas or in spaces between rocks, but in
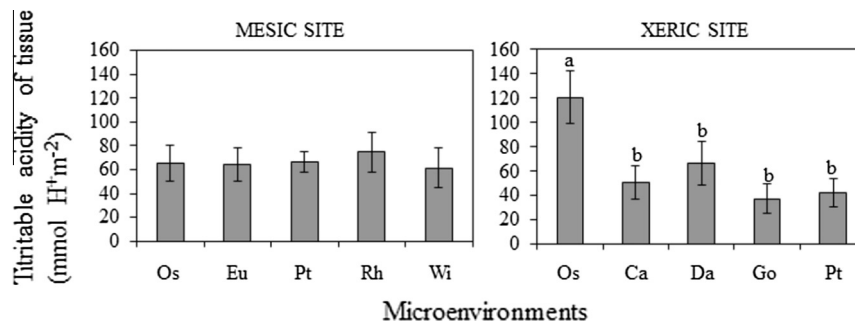
Fig. 4. Total number, production and mortality of leaves (means ± standard errors and confidence intervals) after 337 days of young plants transplanting (2 years old) of *Agave potatorum* and their RGR (in volume), in open spaces and under the canopies of four shrubs in mesic and xeric site. Means followed by different superscript letters are significantly different at $p < 0.05$ by factorial one-way ANOVAs or Kruskal–Wallis tests in cases of leaf production in the mesic site, RGR and leaf production in xeric site. Os = open space, Am = *Amelanchier denticulata*, Ca = *Calliandropsis nervosus*, Eu = *Euphorbia rossiana*, Go = *Gochnatia hypoleuca*, Pt = *Pterostemon rotundifolius*, Rh = *Rhus chondroloma*, Wi = *Wimmeria microphylla*.

Fig. 5. Carbon gain measured as titratable acidity of tissue of *Agave potatorum* (means ± standard errors) in open spaces and under the canopies of nurse plants in the mesic and xeric sites. Means followed by different superscript letters are significantly different at $p < 0.05$ by Kruskal–Wallis tests. Os = open space, Am = *Amelanchier denticulata*, Ca = *Calliandropsis nervosus*, Eu = *Euphorbia rossiana*, Go = *Gochnatia hypoleuca*, Pt = *Pterostemon rotundifolius*, Rh = *Rhus chondroloma*, Wi = *Wimmeria microphylla*.
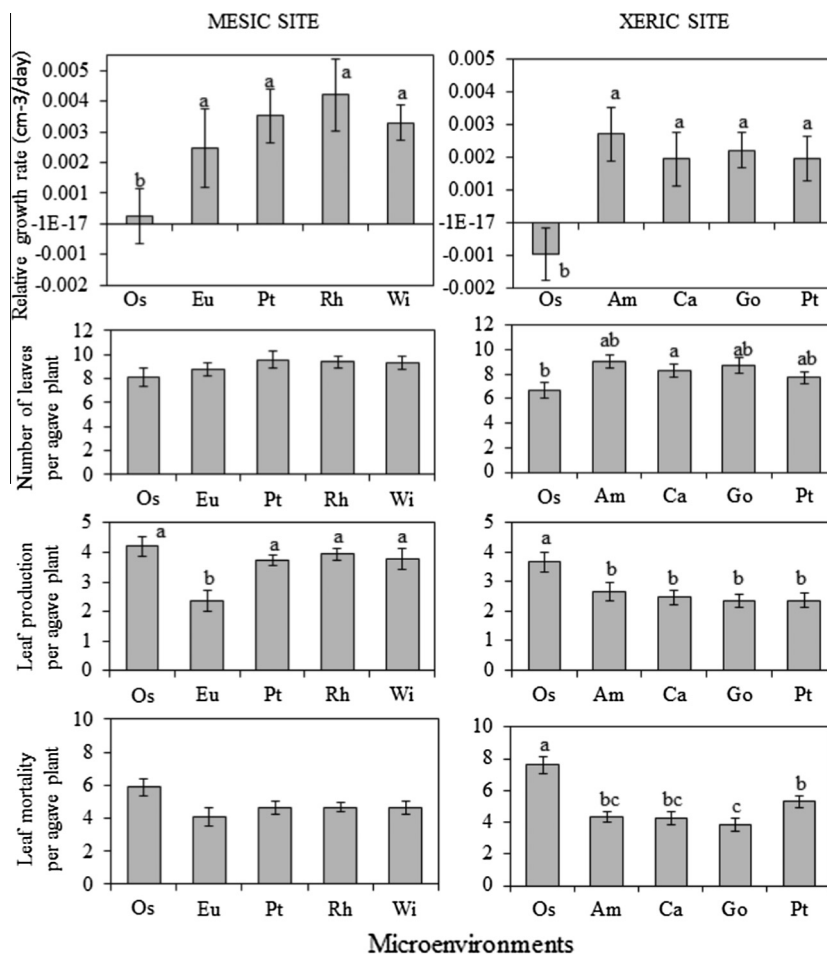
these microenvironments there is a high mortality of seedlings, compared with sites beneath canopies of shrubs (Gómez-Aparicio, 2008; Munguía-Rosas and Sosa, 2008), a pattern that was consistent with results of our research.

The association of *A. potatorum* occurs only with a fraction of the shrub species (29% of species in the mesic site and 36% of species in the xeric site), a slightly lower proportion to that reported

by Valiente-Banuet and Verdú (2007) in biotic communities dominated by columnar cacti, where 34–46% of plant species are nurse plants. We identified significant association with *E. rossiana* and *G. hypoleuca*, which suggests specificity of interaction with these species, probably due to their functional characteristics, their particular form of modifying microenvironments and interactions with other species. All these factors may influence a good performance

and higher survival of *A. potatorum* in different stages of its life cycle (see Callaway, 1998 for a deeper discussion about this topic).

Although in both study sites facilitation is crucial, we expected a higher frequency of the association in the xeric site (Bertness and Callaway, 1994); however, no significant differences were identified in frequency of association between sites even though the strong differences in vegetation physiognomy, environmental temperature and relative humidity (Appendix A). Intraspecific differential adaptations may influence the balance of interactions (Pennings et al., 2003). In the case of *A. potatorum*, the absence of differences in the frequency of facilitation among sites may be due to it is a species with high plasticity (Gentry, 1982) in stress tolerance (Nobel, 1988). However, it is still necessary investigating more about this topic, including more sites that allow visualizing a broader spectrum of environmental conditions. The study sites are only representative of the higher elevations of the range of distribution of *A. potatorum* (García-Mendoza, 2011).

Observations about the differences in colour of agave leaves among sites and the surface occupied by calcareous rocks in the sites allow suggesting that the UV-B radiation incidence, may be determining differential stress of *A. potatorum*, similarly as reported for *A. striata* by Fondom et al. (2009). UV-B radiation causes damage to DNA, photo-oxidation and direct photosynthetic damage, and one plant response is activation of the flavonoid biosynthetic pathway than influence the reflective properties of the leaf surface by anthocyanins production that tend to mask the green chlorophyll pigments and confer a red colour to leaves (Stapleton, 1992). These ecophysiological adaptations may be influencing significantly the interactions of *A. potatorum* with its nurse plants. Studying facilitation as response to stress by UV radiation may be an important research line for further studies (Caldwell and Flint, 1994; Zhang et al., 2012).

Exclusion of predators was the most important factor influencing seedling emergence and survival in the mesic site, contrarily to what occurs in the xeric site where predation only was important for seedling survival. It has been reported that environmental factors such as light intensity and soil humidity significantly influence the presence and density of seed predators (Antvogel and Bonn, 2008). Sites having wide areas without vegetation cover are evaded by seed predators as could occur in the xeric site, where we observed less signs of seed predation. The interaction of predation with microenvironment in seedling survival suggests that predators may have higher incidence in particular microenvironments (Callaway, 1995; Jaksic and Fuentes, 1980), where seedlings are exposed and are more accessible to predators, as we observed in open areas, or where predators find good conditions under the canopies of some particular species. This latter could have been the cases of *E. rossiana* and *P. rotundifolius* in the mesic site or *C. nervosus* and *G. hypoleuca* in the xeric site, where the mortality of seedlings in the not excluded predation treatments occurred more rapidly than in other microenvironments. This result suggests that facilitation in these development steps of *A. potatorum* is dynamic and influenced by differential intensity of factors determining stress among sites (Soliveres et al., 2010).

Effects of microenvironments beneath the canopy of shrubs on seedling emergence were significant only in the mesic site, where we also found strong differences in the environmental temperature and relative humidity among microenvironments. This results suggests that shrubs may have positive effects on germination and that some species have higher quality as nurse plants, in the case studied *R. chondroloma*.

For seedling survival, the microenvironment type was determinant in both sites. Almost all seedlings that survived after one year were those under nurse plants canopies, and we identified shrub species beneath which survival was higher, but the better species varied among sites.

The positive effects of interactions are of particular importance in the development of techniques for enhancing establishment of *A. potatorum* in natural populations through the manual dispersion of seeds beneath the canopies of recognized nurse plants. This practice is recommendable in areas of difficult access where other actions would have high cost (Delgado-Lemus et al., 2014b; Torres et al., 2015).

Seed provenance was important in the treatment of germination under optimal conditions, seedling emergence and survival. Seeds from the xeric site had a better performance in the xeric site, but it was also good in the mesic site. Contrarily, seeds from the mesic site had lower rates of seedling emergency in both sites. This difference could be due to different germination behavior associated to differences in resource storing capacity of the endosperm and the seed coat (Sultan, 2000), as well as in seedling vigor, as it was documented for *Atactorhynchus duranguensis* (Barriada-Bernal et al., 2013).

The percentage of seedling emergence recorded in field experiments were generally lower compared to those recorded for an atypical year of high rainfall in the region (Arizaga and Ezcurra, 2002) and also lower than the optimum conditions simulated in the laboratory. It is worthy to say that during our experiments the rainfall rate was lower than the annual average (260 mm) and we did not record naturally established seedlings in plots where we conducted the experiments, which suggests that germination and successful establishing of *A. potatorum* may be episodic, such as in other species of arid and semiarid areas, during years of rainfall higher than average (Nobel, 1992), which may be 500–600 mm annual in the study site (Quintas, 2000).

In both sites studied, interception of photosynthetic active radiation by shrubs canopy could have negative effects on leaf production, but also positive effects preventing damage on leave tissue, decreasing leaf mortality (Callaway, 1995; Franco and Nobel, 1989; Holmgren et al., 1997). The final balance of these effects was a higher number of leaves and leaf growth rate. Contrarily, agaves transplanted to open áreas had a higher production of new leaves, but in most individuals the high mortality of leaves only allowed recording slight growth or decrease of agaves size. This information suggests that in open spaces the environmental conditions are adverse for agaves, particularly during the first years. This was actually found during our first evaluation of the reforestation carried out by people of San Luis Atolotitlán, before this study. At that time we found that after two years of transplanted, only 44% of agave plants transplanted in open spaces survived, most of them with signs of poor vigor, contrarily to those transplanted under canopy of shrubs where 84% of plants transplanted survived. Unfortunately few agaves (nearly 25%) had been transplanted near or beneath shrub canopies (Casas et al., 2008; Torres et al., 2013).

The significant association of agaves with *E. rossiana* and *G. hypoleuca*, and the negative interaction recorded with *K. cytisoides*, as well as the highest rates of emergence and survival beneath canopy of *R. chondroloma*, suggest that although shade is the principal factor influencing the association, other processes may additionally influence the quality of the different species as nurse plants. However, according to Baumeister and Callaway (2006) and Callaway (1998), the hierarchic influence of other factors become important only when more general mechanisms such as shade do operate. Some of the other factors may be indirect interactions with a third plant species, mycorrhizal fungi, natural enemies, or N fixing bacteria (Van der Heijden and Horton, 2009; Van der Putten, 2009). This situation could be due to a markedly

variable balance of short term interactions (Armas and Pugnaire, 2005; Lloret et al., 2005; Miriti, 2007).

Findings of this study allow new information basic to develop techniques for reforestation and enhancing seedling establishment in wild populations. Our current proposals should be considered for starting adaptive management, in which new experiments, monitoring and evaluation of actions (Grumbine, 1994; Holling, 1978) allow adjusting strategies for the diversity of situations. This approach has the challenge of developing methods to rapid identification of shrub species that are better nurse plants. Transects in conserved areas identifying nurse plant species, presence, absence and number of seedlings, saplings, and adult agaves could be helpful before conducting manual seed dispersion and transplanting of young plants from nurseries. Rapid sampling to determine the spatial distribution of the target species in sites where management actions are going to be conducted may help to understand the resulting effect of the observed variation in the different steps of the life cycle. Such sampling is particularly important in a region like the Tehuacan Valley with high β diversity. The sites of our study were 2 km separated and shared only 30% of shrub species.

Documenting the relation between functional characteristics as the foliar area index, and the variety of mechanisms of facilitation, may help to identify important differences of the nature of stress and how it decreases due to the influence of neighboring plants (Butterfield and Callaway, 2013).

It has been suggested that the close phylogenetic relatedness is a good approach to predict the outcome of plant–plant interactions (Soliveres et al., 2012; Valiente-Banuet and Verdú, 2013, 2008; Verdú et al., 2012). Even more, it has been proposed that for restoration, the minimum phylogenetic distance between nurse and facilitated species to enhance early survival of the latter is around 100 Ma (Verdú et al., 2012). *A. potatorum* is mainly associated with species of the Magnoliopsida, which are on average 163 Ma diverging (Kumar and Hedges, 2011); however we found cases such as the negative interaction with *K. cytisoides* (163 Ma) in the mesic site, as well as the positive interaction with *D. serratifolium*, a closely related species (52 Ma) (Kumar and Hedges, 2011). This information suggests that the phylogenetic distance may provide a first approach for selecting species to be used as nurse plants, but it is also necessary identifying the exceptions.

5. Conclusions

Studies of plant–plant interactions provide key criteria in restoration programmes, and according to our study it is crucial for recovering populations of *A. potatorum*. The assisted reforestation of nurse plants and the target species may have important associated benefits for biodiversity conservation.

The ecological theory may provide important criteria to identify the role of facilitation in the dynamics of species whose recovering is targeted, as well as the causing mechanisms involved.

Shade appears to be a primary factor in facilitation of *A. potatorum*, although other factors (protection against predation and characteristic of the microenvironments) influence the quality of shrubs as nurse plants.

The provenance of seeds influenced the success of seed germination and seedling establishment. Which suggests that local adaptations should be taken into account for planing actions in favour of populations' recovery.

Although deeper studies on mechanisms influencing facilitation, particularly the influence of interactions of other species are still necessary, the results of this study provides helpful information to design strategies for maximizing the benefits of interactions, techniques for improving nursing and transplanting of agaves, selecting the specific nurse plants or simulate their effects.

Local people started actions, some of them successful (seed germination and maintenance of plants in nursery, exclusion of cattle from forest areas), but others unsuccessful (transplanting of agave plants in open areas). Our studies provide useful information for making decisions and actions for protecting and recovering *A. potatorum* populations, but implementation, continual evaluation and adjusting of the better practices according to their success are crucial for ensuring the recovering of populations and its long term utilization. This experience indicates that designing adaptive management strategies together with local people and researchers may be more successful rather than working separately without communication.

Table A.1

Temperature and relative humidity in the mesic and xeric sites. Values are means ± standard error.

		Mesic site	Xeric site
May			
Temperature (°C)	Diurnal	33.097 ± 0.641	24.392 ± 0.480
	Nocturnal	17.689 ± 0.182	14.636 ± 0.176
Relative humidity (%)	Diurnal	37.935 ± 1.762	48.663 ± 1.714
	Nocturnal	60.999 ± 0.230	73.392 ± 0.949
June			
Temperature (°C)	Diurnal	28.474 ± 0.150	28.491 ± 1.408
	Nocturnal	14.331 ± 0.098	11.738 ± 0.144
Relative humidity (%)	Diurnal	36.065 ± 1.132	38.029 ± 0.720
	Nocturnal	75.447 ± 0.414	82.919 ± 0.490

Environmental conditions in sites mesic and xeric were measured with HOBO H8 sensors (Onset Computer Corporation, Massachusetts, USA) located in three sampling stations per site distributed in open spaces. These sensors recorded simultaneously temperature, relative humidity and light every five minutes for 24 h.

Table A.2
Environmental and soil characteristics in the microenvironments used for testing emergence, survival, CO_2 absorption, and growth in the mesic and xeric sites. Values are means ± standard error. Means followed by different superscript letters are significantly different at $p < 0.05$.

Site	Microenvironment					Data analysis
	Open space	Euphorbia rossiana 1.5 m height, perennial foliage of 1.6 m	Pterostemon rotundifolius 1.7 m height, seasonal foliage of 2.1 m^{-2}	Rhus chondroloma 1.3 m height, perennial foliage of 2.5 m^{-2}	Wimmeria microphylla 1.3 m height, seasonal foliage of 1.2 m^{-2}	
Mesic site **Environment June** **Temperature (°C)**						
Diurnal	25.88 ± 0.24	21.92 ± 0.39	–	23.18 ± 0.15	–	
Nocturnal	14.34 ± 0.15	14.97 ± 0.024	–	14.75 ± 0.047	–	
Relative humidity (%)						
Diurnal	39.91 ± 0.146	49.05 ± 0.87	–	45.85 ± 0.190	–	
Nocturnal	74.24 ± 0.02	72.44 ± 0.34	–	72.19 ± 0.65	–	
Light intensity (lumens/ft^{-2})	837.19 ± 48.36	398.61 ± 90.32	–	590.81 ± 14.32	–	
Soil						
Clay (%)	17.80 ± 2.00	18.47 ± 2.40	19.13 ± 1.33	19.80 ± 0.00	19.80 ± 0.00	$F = 0.346$, $df = 4.10$, $p = 0.841$
Silt (%)	20.67 ± 3.33	23.34 ± 1.76	26.00 ± 2.00	23.33 ± 1.76	25.33 ± 0.67	$F = 0.999$, $df = 4.10$, $p = 0.452$
Sand (%)	61.53 ± 5.33	58.21 ± 4.00	54.87 ± 1.76	56.87 ± 1.76	54.87 ± 0.67	$F = 0.757$, $df = 4.10$, $p = 0.576$
Field capacity (%)	14.23 ± 2.20	15.43 ± 2.02	16.60 ± 0.80	16.24 ± 0.53	16.84 ± 0.21	$F = 0.570$, $df = 4.10$, $p = 0.691$
pH	7.83 ± 0.04	7.80 ± 0.04	7.77 ± 0.08	7.72 ± 0.11	7.91 ± 0.06	$F = 0.951$, $df = 4.10$, $p = 0.475$
Organic matter (%)	8.13 ± 0.36	9.59 ± 1.88	9.81 ± 0.73	12.08 ± 2.49	9.65 ± 1.96	$F = 0.669$, $df = 4.10$, $p = 0.628$
Ammonia nitrogen (ppm)	6.99 ± 3.63	9.24 ± 2.60	3.83 ± 0.98	5.86 ± 2.88	8.79 ± 4.13	$F = 0.529$, $df = 4.10$, $p = 0.718$
Mineral nitrogen (ppm)	8.68 ± 3.51	11.04 ± 2.81	4.25 ± 1.25	4.21 ± 0.64	10.15 ± 4.33	$F = 1.287$, $df = 4.10$, $p = 0.339$
Phosphorus (ppm)	6.89 ± 0.49	6.12 ± 1.29	5.86 ± 0.71	5.64 ± 0.41	6.40 ± 0.35	$F = 0.444$, $df = 4.10$, $p = 0.775$
Potassium (ppm)	154.28 ± 29.41	221.71 ± 71.70	142.18 ± 9.11	187.37 ± 21.05	194.01 ± 36.18	$F = 0.651$, $df = 4.10$, $p = 0.639$
Calcium (ppm)	7700.00 ± 583.79	7466.67 ± 384.41	6883.33 ± 142.40	7466.67 ± 187.82	8083.33 ± 174.00	$F = 1.656$, $df = 4.10$, $p = 0.236$
Magnesium (ppm)	620.00 ± 276.22	620.00 ± 199.99	240.00 ± 51.96	520.00 ± 36.05	600.00 ± 121.24	$F = 0.970$, $df = 4.10$, $p = 0.465$
Carbonates (%)	12.28 ± 0.03	12.28 ± 0.03	12.14 ± 0.14	12.08 ± 0.17	12.27 ± 0.14	$F = 0.648$, $df = 4.10$, $p = 0.641$
	Open space	Calliandropsis nervosus 0.35 m height, seasonal foliage of 0.3 m^{-2}	Amelanchier denticulata 0.4 m height, seasonal foliage of 0.9 m^{-2}	Gochnatia hypoleuca 0.6 m height, perennial foliage of 0.6 m^{-2}	Pterostemon rotundifolius 0.7 m height, seasonal foliage of 0.8 m^{-2}	
Xeric site **Environment June** **Temperature (°C)**						
Diurnal	27.57 ± 0.73	–	–	22.93 ± 1.66	22.87 ± 0.11	
Nocturnal	10.92 ± 0.27	–	–	11.78 ± 0.24	11.84 ± 0.03	
Relative humidity (%)						
Diurnal	38.67±.12	–	–	43.25 ± 2.74	43.29 ± 0.26	
Nocturnal	81.62 ± 0.57	–	–	79.30 ± 0.20	79.83 ± 0.66	
Light intensity (lumens/ft^{-2})	921.86 ± 11	–	–	825.96 ± 109.46	648.61 ± 39.43	

Table A.2 (*continued*)

Site	Microenvironment					Data analysis
	Open space	*Euphorbia rossiana* 1.5 m height, perennial foliage of 1.6 m	*Pterostemon rotundifolius* 1.7 m height, seasonal foliage of 2.1 m^{-2}	*Rhus chondroloma* 1.3 m height, perennial foliage of 2.5 m^{-2}	*Wimmeria microphylla* 1.3 m height, seasonal foliage of 1.2 m^{-2}	
Soil						
Clay (%)	19.13 ± 1.76[b]	19.13 ± 0.67[b]	17.80 ± 2.31[b]	13.13 ± 0.67[ab]	11.13 ± 1.33[a]	$F = 6.566$, $df = 4.10$, $p = 0.007$
Silt (%)	22.67 ± 1.33	24.67 ± 0.67	24.67 ± 2.91	23.33 ± 0.67	24.67 ± 1.33	$F = 0.340$, $df = 4.10$, $p = 0.845$
Sand (%)	58.20 ± 2.00	56.20 ± 1.16	57.53 ± 4.37	63.53 ± 0.67	64.20 ± 2.31	$F = 2.220$, $df = 4.10$, $p = 0.14$
Field capacity (%)	15.61 ± 1.17[ab]	16.19 ± 0.58[b]	15.38 ± 1.99[ab]	11.93 ± 0.36[ab]	11.10 ± 1.04[a]	$F = 3.985$, $df = 4.10$, $p = 0.035$
pH	7.65 ± 0.09	7.82 ± 0.04	7.82 ± 0.05	7.80 ± 0.05	7.70 ± 0.03	$F = 2.083$, $df = 4.10$, $p = 0.158$
Organic matter (%)	13.88 ± 1.61	9.09 ± 0.43	10.33 ± 1.62	12.64 ± 0.53	12.50 ± 1.29	$F = 2.672$, $df = 4.10$, $p = 0.095$
Ammonia nitrogen (ppm)	7.44 ± 1.41[b]	34.49 ± 8.12[a]	15.56 ± 2.74[ab]	19.39 ± 3.93[ab]	46.90 ± 18.55[a]	$F = 3.542$, $df = 4.10$, $p = 0.048$
Mineral nitrogen (ppm)	8.59 ± 1.26[b]	30.25 ± 7.92[a]	17.32 ± 2.75[ab]	20.54 ± 3.93[ab]	52.62 ± 17.35[a]	$F = 5.522$, $df = 4.10$, $p = 0.013$
Phosphorus (ppm)	7.82 ± 1.21	7.40 ± 1.03	8.24 ± 0.69	7.14 ± 0.49	6.99 ± 1.15	$F = 0.285$, $df = 4.10$, $p = 0.881$
Potassium (ppm)	211.37 ± 3.47	180.32 ± 38.66	246.15 ± 34.77	329.18 ± 71.60	341.33 ± 67.22	$F = 2.052$, $df = 4.10$, $p = 0.163$
Calcium (ppm)	9433.33 ± 2333.45	7716.67 ± 622.67	9183.33 ± 2233.46	12500.00 ± 435.88	8566.67 ± 3686.06	$F = 0.668$, $df = 4.10$, $p = 0.628$
Magnesium (ppm)	890.00 ± 121.65[b]	590.00 ± 183.57[b]	1120.00 ± 259.42[b]	1080.00 ± 147.98[b]	7400.00 ± 1259.29[a]	$F = 24.489$, $df = 4.10$, $p < 0.001$
Carbonates (%)	26.02 ± 7.60	36.34 ± 0.19	21.65 ± 1.16	21.82 ± 1.68	26.58 ± 4.91	$F = 2.069$, $df = 4.10$, $p = 0.16$

Environmental conditions in microsites were measured with HOBO H8 sensors (Onset Computer Corporation, Massachusetts, USA) located in two sampling stations per microsite per site. They recorded simultaneously temperature, relative humidity and light every five minutes for 24 h.

Appendix A

Description of the environmental characteristics of the mesic and xeric sites studied, and those of the microenvironments used for testing emergence, survival, CO_2 absorption and growth (see Tables A.1 and A.2).

Three soil samples by microenvironment were collected from upper 15 cm of the soil in each site. Clay, silt and sand by were determined by the Bouyoucos hydrometer method; field capacity was estimated. Soil pH was measured with an Accumet AR20 pH meter (Fisher Scientific Company, Pittsburgh, Pennsylvania, USA). Organic matter was measured. Ammonia nitrogen was measured by the Nessler method and mineral nitrogen by spectrophotometry (Spectronic 21D, Milton Roy, Rochester, New York, USA). Water-soluble phosphorus was estimated by ultraviolet–visible spectrophotometry (Spectronic 21D, Milton Roy, Rochester, New York, USA); potassium was measured by spectrophotometry (Flame photometer Cole-Parmer 2655-00, Cole-Parmer Instrument Co., Chicago, Illinois, E.U.); calcium and magnesium were measured volumetrically with EDTA; and carbonates percentage by volumetric analysis.

Differences in soil characteristics were tested through factorial one-way ANOVAs by variable and per site, Tukey multiple range tests were performed for significant differences, these analyses were conducted with STATISTICA 6 (StatSoft-Inc., 2003). Variables expressed in percentage were arcsine square root transformed.

Appendix B

Microenvironments surface, number of *Agave potatorum* plants of the categories seedling–sapling and adults associated to each microenvironment, and relative interaction index (RII) in the mesic and xeric sites based on number of individuals m^{-2}.

Microenvironment		Mesic site					Xeric site				
Family	Specie	Total microenvironment cover (%)	Seedling and sapling plants (number)	Adult plants (number)	Total *Agave* plants (ind/ m^{-2})	RII	Total microenvironment cover (%)	Seedling and sapling plants (number)	Adult plants (number)	Total *Agave* plants (ind/ m^{-2})	RII
Acanthaceae		0.01	0	0	<0.01	−1	–	–	–	–	–
Adiantaceae		0.02	0	0	<0.01	−1	–	–	–	–	–
Agavaceae	*Agave kerchovei*	0.05	0	0	<0.01	−1	0.14	0	0	<0.01	−1
Agavaceae	*Agave salmiana*	0.21	0	0	<0.01	−1	0.02	0	0	<0.01	−1
Agavaceae	*Agave* sp.	0.53	0	0	<0.01	−1	0.36	0	0	<0.01	−1
Agavaceae	*Yucca periculosa*	0.11	0	0	<0.01	−1	–	–	–	–	–
Anacardiaceae	*Actinocheita potentillifolia*	0.20	0	0	<0.01	−1	<0.01	0	0	<0.01	−1
Anacardiaceae	*Pseudosmodingium multifolium*	–	–	–	–	–	<0.01	0	0	<0.01	−1
Anacardiaceae	*Rhus chondroloma*	8.43	7	8	0.07	0.33	–	–	–	–	–
Araliaceae	*Aralia humilis*	<0.01	0	0	<0.01	−1	–	–	–	–	–
Asteraceae	*Ageratina espinosarum*	3.22	4	1	0.06	0.27	0.82	3	2	0.24	0.78
Asteraceae	*Ageratina hebes*	1.42	2	0	0.06	0.22	0.04	0	0	<0.01	−1
Asteraceae		0.72	1	0	0.06	0.22	–	–	–	–	–
Asteraceae		–	–	–	–	–	0.12	0	2	0.65	0.91
Asteraceae		–	–	–	–	–	0.16	0	0	<0.01	−1
Asteraceae		–	–	–	–	–	0.72	8	3	0.62	0.91
Asteraceae		–	–	–	–	–	0.07	0	0	<0.01	−1
Asteraceae		–	–	–	–	–	0.24	1	0	0.17	0.70
Asteraceae	*Brickellia veronicifolia*	–	–	–	–	–	0.09	0	0	<0.01	−1
Asteraceae	*Gochnatia hypoleuca*	–	–	–	–	–	11.18	32	48	0.29	0.81
Asteraceae	*Gymnosperma glutinosum*	0.03	0	0	<0.01	−1	0.46	1	1	0.17	0.71
Asteraceae	*Perymenium discolor*	3.13	5	5	0.13	0.56	0.65	2	5	0.43	0.87
Asteraceae	*Pittocaulon praecox*	0.21	0	0	<0.01	−1	<0.01	0	0	<0.01	−1
Asteraceae	*Verbesina* sp.	0.39	0	0	<0.01	−1	0.69	0	0	<0.01	−1
Asteraceae	*Verbesina* sp.	0.20	0	0	<0.01	−1	0.18	0	0	<0.01	−1
Asteraceae	*Viguiera pinnatilobata*	0.31	0	0	<0.01	−1	0.18	0	0	<0.01	−1
Asteraceae	*Zexmenia pringlei*	–	–	–	–	–	0.02	0	0	<0.01	−1
Bignoniaceae	*Tecoma stans*	0.01	0	0	<0.01	−1	<0.01	0	0	<0.01	−1
Bromeliaceae	*Hechtia* sp.	2.29	3	2	0.09	0.42	0.46	0	1	0.09	0.49
Bromeliaceae	*Tillandsia* sp.	<0.01	0	0	<0.01	−1	–	–	–	–	–
Burseraceae	*Bursera* sp.	6.32	6	3	0.06	0.23	–	–	–	–	–
Cactaceae	*Ferocactus flavovirens*	0.25	0	0	<0.01	−1	–	–	–	–	–
Cactaceae	*Lophocereus marginatus*	<0.01	0	0	<0.01	−1	–	–	–	–	–

Microenvironment		Mesic site					Xeric site				
Family	Specie	Total microenvironment cover (%)	Seedling and sapling plants (number)	Adult plants (number)	Total *Agave* plants (ind/m^{-2})	RII	Total microenvironment cover (%)	Seedling and sapling plants (number)	Adult plants (number)	Total *Agave* plants (ind/m^{-2})	RII
Cactaceae	*Mammillaria sphacelata*	–	–	–	–	–	0.01	0	0	<0.01	−1
Cactaceae	*Opuntia pilifera*	0.72	0	0	<0.01	−1	0.07	0	0	<0.01	−1
Celastraceae	*Wimmeria pubescens*	10.20	13	15	0.11	0.51	–	–	–	–	–
Convolvulaceae	*Ipomoea arborescens*	0.22	0	0	<0.01	−1	–	–	–	–	–
Cupressaceae	*Juniperus flaccida*	<0.01	0	0	<0.01	−1	–	–	–	–	–
Ephedraceae	*Ephedra compacta*	–	–	–	–	–	0.06	0	0	<0.01	−1
Euphorbiaceae	*Cnidosculus tehuacanensis*	<0.01	0	0	<0.01	−1	–	–	–	–	–
Euphorbiaceae	*Croton ciliatoglandulifer*	0.01	0	0	<0.01	−1	–	–	–	–	–
Euphorbiaceae	*Croton rzedowskii*	0.55	0	0	<0.01	−1	–	–	–	–	–
Euphorbiaceae	*Euphorbia rossiana*	14.13	41	17	0.16	0.64	–	–	–	–	–
Euphorbiaceae		0.09	0	0	<0.01	−1	0.01	0	0	<0.01	−1
Euphorbiaceae	*Jatropha dioica*	0.11	0	0	<0.01	−1	–	–	–	–	–
Flacourtiaceae	*Neopringlea viscosa*	2.95	1	2	0.04	0.06	0.07	1	0	0.59	0.90
Krameriaceae	*Krameria cytisoides*	6.54	1	1	0.01	−0.49	1.40	0	2	0.06	0.32
Lamiaceae		0.05	0	0	<0.01	−1	–	–	–	–	–
Lamiaceae	*Salvia candicans*	0.09	0	0	<0.01	−1	1.48	2	1	0.08	0.47
Lamiaceae	*Salvia thymoides*	–	–	–	–	–	0.87	2	1	0.14	0.64
Leguminosae	*Bauhinia deserti*	0.15	0	0	<0.01	−1	–	–	–	–	–
Leguminosae	*Calliandropsis nervosus*	0.04	0	0	<0.01	−1	2.41	2	11	0.22	0.76
Leguminosae	*Dalea* sp.	2.14	3	1	0.07	0.35	0.07	8	0	4.87	0.99
Leguminosae	*Dalea* sp.	1.09	1	0	0.04	0.01	0.03	1	0	1.47	0.96
Leguminosae	*Eysenhardtia polystachya*	1.93	2	1	0.06	0.27	0.05	0	0	<0.01	−1
Leguminosae		0.05	0	1	0.77	0.91	0.04	0	0	<0.01	−1
Leguminosae		–	–	–	–	–	0.04	0	0	<0.01	−1
Leguminosae		–	–	–	–	–	0.03	0	0	<0.01	−1
Leguminosae	*Mimosa luisana*	0.52	0	2	0.15	0.62	–	–	–	–	–
Leguminosae	*Mimosa* sp.	2.77	8	1	0.13	0.57	0.05	0	0	<0.01	−1
Leguminosae		–	–	–	–	–	0.01	0	0	<0.01	−1
Leguminosae		–	–	–	–	–	0.06	0	0	<0.01	−1
Leguminosae		–	–	–	–	–	1.32	0	5	0.15	0.67
Leguminosae	*Senna galeottiana*	4.73	5	5	0.08	0.40	–	–	–	–	–
Leguminosae	*Senna* sp.	0.01	0	0	<0.01	−1	0.18	0	0	<0.01	−1
Malpighiaceae	*Galphimia glauca*	0.02	0	0	<0.01	−1	0.11	0	0	<0.01	−1
Nolinaceae	*Dasylirion serratifolium*	0.97	3	2	0.21	0.70	2.48	6	5	0.18	0.71
Oleaceae	*Fraxinus purpusii*	0.03	0	0	<0.01	−1	–	–	–	–	–

Microenvironment		Mesic site					Xeric site				
Family	Specie	Total microenvironment cover (%)	Seedling and sapling plants (number)	Adult plants (number)	Total *Agave* plants (ind/m^{-2})	RII	Total microenvironment cover (%)	Seedling and sapling plants (number)	Adult plants (number)	Total *Agave* plants (ind/m^{-2})	RII
Rosaceae	*Amelanchier denticulata*	0.64	0	1	0.06	0.27	3.40	1	6	0.08	0.47
Rosaceae	*Xerospirea hartwegiana*	–	–	–	–	–	0.36	0	0	<0.01	−1
Rubiaceae	*Bouvardia longiflora*	1.28	2	3	0.16	0.63	0.30	2	2	0.53	0.89
Rutaceae	*Zanthoxylum* sp.	0.31	0	0	<0.01	−1	–	–	–	–	–
Sapindaceae	*Dodonaea viscosa*	0.14	0	0	<0.01	−1	0.03	0	0	<0.01	−1
Saxifragaceae	*Pterostemon rotundifolius*	8.21	14	11	0.12	0.54	1.83	12	2	0.31	0.82
Scrophulariaceae	*Penstemon campanulatus*	–	–	–	–	–	0.59	1	1	0.14	0.64
Scrophulariaceae	*Russelia coccinea*	0.03	0	0	<0.01	−1	–	–	–	–	–
Simaroubaceae	*Castela tortuosa*	–	–	–	–	–	0.45	0	0	<0.01	−1
Turneraceae	*Turnera diffusa*	0.13	0	0	<0.01	−1	–	–	–	–	–
Verbenaceae	*Lantana* sp.	0.03	0	0	<0.01	−1	–	–	–	–	–
Verbenaceae	*Lippia graveolens*	<0.01	0	0	<0.01	−1	–	–	–	–	–
Verbenaceae	*Lippia oaxacana*	0.04	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.13	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.01	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.01	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.20	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.03	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.03	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.01	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.08	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.01	0	0	<0.01	−1	–	–	–	–	–
Undetermined		<0.01	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.14	0	0	<0.01	−1	–	–	–	–	–
Undetermined		<0.01	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.05	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.02	0	0	<0.01	−1	–	–	–	–	–
Undetermined		0.15	0	0	<0.01	−1	–	–	–	–	–
Undetermined		–	–	–	–	–	0.03	0	0	<0.01	−1
Undetermined		–	–	–	–	–	<0.01	0	0	<0.01	−1
Undetermined		–	–	–	–	–	0.01	0	0	<0.01	−1
Undetermined		–	–	–	–	–	0.01	0	0	<0.01	−1
Undetermined		–	–	–	–	–	<0.01	0	0	<0.01	−1
Undetermined		–	–	–	–	–	0.03	0	0	<0.01	−1
Undetermined		–	–	–	–	–	0.77	0	0	<0.01	−1
	Dead srhubs	0.09	5	8	6.01	0.99	0.03	3	2	6.51	0.99
	Open space	10.04	7	2	0.04	0	64.72	25	21	0.03	0

Appendix C

Rates of starting survival (linear parameter), throughout time (linear parameter) and throughout quadratic time of the seedling survival of seeds from the mesic and xeric sites, in open spaces and beneath canopies of shrubs with and without predator exclusions.

Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.03. 003. These data include Google maps of the most important areas described in this article.

Site	Microenvironment	Starting survival rate		Survival rate throughout time		Survival rate throughout quadratic time	
		With exclusion	Without exclusion	With exclusion	Without exclusion	With exclusion	Without exclusion
Mesic site							
Mesic site seeds	Open spaces	−2.475	−3.699	−0.397	−0.397		
	Euphorbia rossiana	−2.189	−5.318	−0.397	−0.397		
	Pterostemon rotundifolius	−1.975	−4.400	−0.397	−0.397		
	Rhus chondroloma	−1.451	−2.834	−0.397	−0.397		
	Wimmeria microphylla	−2.394	−3.140	−0.397	−0.397		
Xeric site seeds	Open spaces	−2.097	−3.321	−0.397	−0.397		
	Euphorbia rossiana	−1.811	−4.940	−0.397	−0.397		
	Pterostemon rotundifolius	−1.597	−4.021	−0.397	−0.397		
	Rhus chondroloma	−1.073	−2.456	−0.397	−0.397		
	Wimmeria microphylla	−2.015	−2.761	−0.397	−0.397		
Xeric site							
Xeric site seeds	Open spaces	−1.755	−1.879	−0.003	−0.172	−0.035	−0.035
	Calliandropsis nervosus	−3.482	−1.151	−0.194	−3.260	−0.035	−0.035
	Amelanchier denticulata	−4.978	−3.476	−0.118	−0.456	−0.035	−0.035
	Gochnatia hypoleuca	−3.103	−11.030	−0.129	−1.241	−0.035	−0.035
	Pterostemon rotundifolius	−2.648	−13.490	0.0607	−0.053	−0.035	−0.035
Mesic site seeds	Open spaces	−3.250	−3.950	−0.003	−0.172	−0.035	−0.035
	Calliandropsis nervosus	−2.638	0.964	−0.194	−3.260	−0.035	−0.035
	Amelanchier denticulata	−2.559	−2.540	−0.118	−0.456	−0.035	−0.035
	Gochnatia hypoleuca	−1.822	−3.433	−0.129	−1.241	−0.035	−0.035
	Pterostemon rotundifolius	−2.349	−2.252	0.0607	−0.053	−0.035	−0.035

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