



# Hierarchical effects of rainfall, nurse plants, granivory and seed banks on cactus recruitment

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## Keywords

Conditionality; Density; Facilitation; Granivory; Nurse plant; *Pachycereus schottii*; Precipitation; Recruitment; Seed bank; Senita cactus; Species composition

## Nomenclature

Turner et al. (2001)

Received 20 May 2012

Accepted 24 October 2012

Co-ordinating Editor: Michael Huston

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## Abstract

**Aims:** Plant facilitation is recognized as an important process, contributing not only to the ecology of individual species, but the diversity, organization and stability of communities as a whole. While decades of studies have enhanced our knowledge of the mechanisms contributing to plant facilitation, greater attention is now being given to the conditionality of the mechanisms, whereby multiple biotic and abiotic factors may act independently and jointly with one another in shaping plant–plant facilitation. Our objective was to evaluate the conditionality and hierarchy of mechanisms contributing to cactus germination and early seedling recruitment arising from plant–plant facilitation, including the effects of seed banks, rainfall, granivory and nurse plants.

**Location:** Bahía de Kino, Sonora, Mexico; Sonoran Desert of North America.

**Methods:** We employed descriptive analyses and a factorial experiment to examine the consequences of rainfall, nurse plants, granivory and seed banks for senita cactus recruitment (*Pachycereus schottii*) in two plant communities of the Sonoran Desert: one degraded of its key nurse plants and the other with its nurse plants intact.

**Results:** Seed banks did not occur in either of the plant communities, indicating that seed banks and seed dormancy do not affect senita recruitment and thereby do not modulate other mechanisms that contribute to nurse plant facilitation and cactus recruitment. Juvenile senita cacti were consistently associated with nurse plants in both plant communities. Yet, the density and species composition of nurse plants differed between the communities, resulting in reduced senita recruitment and shifts to alternative nurse plants in the community degraded of its key nurse plants compared to the intact community. In a factorial experiment manipulating rainfall, granivory and nurse plants, we found that rainfall and granivory had significant main factor effects, leading to increases and decreases in seedling recruitment, respectively. There was no main factor effect of nurse plants, but there was a significant nurse plant by granivory interaction, indicating that nurse plants increase seedling recruitment through escape from granivory conditional upon rainfall.

**Conclusions:** Taken together, these results reveal a conditional hierarchy of mechanisms of plant–plant facilitation shaping senita cactus recruitment, namely the predominant effects of rainfall increasing recruitment and of granivory decreasing recruitment, for which nurse plants played a key role in increasing seedling recruitment with rainfall and by reducing granivory.

## Introduction

Although the negative effects of competition are commonly emphasized in community ecology, in recent decades the prominence of facilitation has increased – a

process in which one species has a positive effect on one or more demographic rates (e.g. growth, recruitment, survival, reproduction) of another species (Bertness & Callaway 1994; Callaway 1995; Bruno et al. 2003; Stachowicz 2001; Brooker et al. 2008; Brooker & Callaway 2009). Like

the negative effects of competition, the positive feedback of facilitation can have key ecological effects, ranging from the structure and dynamics of populations to the diversity, organization and stability of communities (Stachowicz 2001; Valiente-Banuet et al. 2002; Bruno et al. 2003; Callaway 2007; Butterfield 2009). Diverse mechanisms of facilitation in ecological communities have now been identified, including one species altering the supply of resources, such as nutrients, light and water, to another species; one species buffering abiotic factors such as frost, wind and heat that are intolerable for another species; and one species protecting another from its natural enemies, such as herbivores and granivores (Callaway 1995, 2007).

The positive effects of facilitation may vary with the community context, whereby abiotic and biotic conditions can modulate the positive effects of facilitation (Callaway & King 1996; Callaway et al. 1996; Bruno et al. 2003; Baumeister & Callaway 2006; Altieri et al. 2007; Alberti et al. 2008; Zimmermann et al. 2008). The conditionality of facilitation is recognized to shift facilitation back and forth to competition with environmental stress and productivity gradients (Bertness & Callaway 1994; Bruno et al. 2003). For example, facilitative plant–plant interactions can shift to antagonistic competitive interactions depending on where along the abiotic water stress gradient interactions take place in desert environments (Holmgren et al. 1997; McCluney et al. 2011). More attention is being paid to how multiple biotic and abiotic conditions can shape the positive effects of facilitation. Baumeister & Callaway (2006) have elegantly shown that different mechanisms of facilitation can function in a hierarchical manner, such that one mechanism of facilitation may only be influential in the presence or absence of another. Such key results indicate that studies of one mechanism of facilitation in isolation from other mechanisms may not accurately reflect their role in nature.

One of the best known cases of facilitative interactions is enhanced recruitment and performance of plants under perennial shrubs and trees, known as nurse plants (Sosa & Fleming 2002; Valiente-Banuet et al. 2002; Godínez-Álvarez et al. 2003). Facilitation by nurse plants is critical for cactus recruitment, whereby perennial shrubs and trees enhance germination and seedling establishment through a variety of mechanisms, including attracting seed dispersers as roosts, providing shade and light environments that reduce evapotranspiration, reducing granivory and herbivory, increasing soil nutrients and reducing extreme soil temperatures (Franco & Nobel 1989; Valiente-Banuet & Ezcurra 1991; Rojas-Aréchiga & Vázquez-Yanes 2000; Mandujano et al. 2002; Sosa & Fleming 2002; Valiente-Banuet et al. 2002; Godínez-Álvarez et al. 2003; Drezner 2006; Callaway 2007). Mechanisms in nurse plant facilitation of cactus recruitment may well be conditional upon

the community context of the plant–plant interactions, as historical studies of the giant saguaro cactus (*Carnegiea gigantea*) point to the interdependence of water, shade, frost, temperature and granivory in the survival and recruitment of seedlings (Turner et al. 1966, 1969; Steenbergh & Lowe 1969).

We examined nurse plant facilitation and its conditionality for senita cactus (*Pachycereus schottii*) recruitment in the Sonoran Desert. We evaluated the influences of rainfall, granivory, nurse plants and seed banks for senita recruitment in two communities: one with its nurse plants intact and the other degraded of its key nurse plants. We tested the extent to which recruitment and nurse plant associations differed between these two plant communities given the composition of their nurse plant species. We also examined seed banks in the open desert and beneath nurse plants to assess their ongoing influence relative to other biotic and abiotic factors. We conducted a factorial experiment to test how germination and initial seedling recruitment of senita cacti varies with the independent and joint effects of rainfall, granivory and nurse plants.

## Methods

### Study system

During spring and summer months of 2009, 2010 and 2011, we studied the recruitment of senita cacti (*P. schottii*, Cactaceae) in the Sonoran Desert of Mexico, near Bahia de Kino, Sonora, Mexico. Rainfall regimes in arid environments are characterized by increasing intra- and inter-annual variability with decreasing annual precipitation (Davidowitz 2002). On the Gulf of California along one of the drier regions of the Sonoran Desert, Bahia de Kino receives <50 to 279 mm·yr<sup>-1</sup> of rainfall, with a mean ( $\pm 1$  SD) of  $126 \pm 72$  mm·yr<sup>-1</sup> (1974–1993; DICTUS, Bahia de Kino, Sonora, Mexico). We studied senita cacti at two study sites near Bahia de Kino: Seri Flats (28°52' 35.14" N, 111°57'18.29" W) and Polilla Flats (28°53' 24.73" N, 111°56'38.70" W). Seri Flats is 45 ha in area, while Polilla Flats is much smaller at 7 ha. Seri Flats is more easily accessed and closer (4 km) to Bahia de Kino than Polilla Flats. As a result, harvesting of nurse plants such as mesquite (*Prosopis glandulosa*) and ironwood (*Olneya tesota*) for firewood, charcoal and wood-carving (Suzán et al. 1994) has been higher over the past three decades at Seri Flats than Polilla Flats (F. Molina-Freaner & J.N. Holland, pers. obs.). Senita is a long-lived (>75 yrs), multi-stemmed columnar cactus that reaches heights of 4–5 m. Plants produce thousands of buds, flowers and fruits from spine-bearing areoles during flowering seasons from April to August. Senita cacti rely on the obligate pollinating, seed-eating senita moth (*Upiga virescens* Hulst; Lepidoptera: Cambidae) for pollination and reproduction, as

senita cacti are self-incompatible and co-pollinators are rarely influential (Holland 2002; Holland & Fleming 2002). Mature berry-like fruits contain 160 seeds and are bird-dispersed. Seed germination is >95% in the laboratory (Holland & Fleming 1999a), suggesting that the dormancy rate is low to absent.

### Field survey of nurse plants

Following Valiente-Banuet et al. (1991), we assessed whether senita cacti associate with nurse plants and if senita recruitment and nurse plant associations differed between Seri Flats and Polilla Flats. Briefly, this method is based on measuring distances from juvenile cacti to potential nurse plants and assessing if those distances are shorter than distances of random points to potential nurse plants. At each study site, we walked a grid covering the entire site, censusing for juvenile senita cacti (<1.2 m in height). For each juvenile, we measured the distance (to nearest 0.05 m) to the edge of the canopy of the nearest potential nurse plant. The distance was zero when senita were under the canopy. We calculated the mode and median distances for juvenile senita cacti to each nurse plant species, together with a mean distance and SE. We established 60 and 50 random points at Seri Flats and Polilla Flats, respectively, to measure expected distances to nurse plant species. Random points were established using randomly generated latitudes and longitudes, each of which was located using a 12-satellite SBAS GPS unit (Magellan Mobile Mapper). For Seri Flats, we obtained 430 observed and 425 expected distances to nurse plants, and for Polilla Flats we obtained 261 observed and 276 expected distances for nurse plants. To test if observed distances were shorter than expected distances, we used a two sample *t*-test with pooled variance between the observed and expected distances. We conducted the statistical tests for all nurse plants pooled as a group, and for each species of nurse plant individually. All statistics here and below were conducted with R (R Development Core Team 2009; R Foundation for Statistical Computing, Vienna, AT, US). Note, we did not test each of the many different mechanisms of nurse plant facilitation for each individual nurse plant species, as many studies have shown these positive effects on cacti (Godínez-Álvarez et al. 2003; Callaway 2007).

### Field survey of seed bank

Little is known of seed banks of Cactaceae, or their potential contribution to cactus recruitment. We examined whether cactus seed banks were present at each of the study sites, which could in turn modulate other mechanisms contributing to cactus recruitment and nurse plant facilitation. Based on the random sampling points at each

study site, ten soil samples were collected from beneath each nurse plant species, from the open desert and from under senita cacti. Soil samples were collected prior to fruit production, so that seeds in the soil samples were from the previous years' fruit crops. Each soil sample consisted of two soil cores of 15 cm in diameter and 5 cm in depth, which is recommended based on depths of seeds in desert soils (Kemp 1989; Csontos 2007). Soil samples were carefully sieved (1 mm) and inspected for cactus seeds, including senita (*P. schottii*), cardon (*P. pringlei*), organ pipe (*Stenocereus thurberi*) and saguaro (*Carnegiea gigantea*). We did not distinguish among the four species because few to no seeds were observed, suggesting the lack of a soil seed bank. We assessed viability of seeds collected through germination trials in Petri dishes for 12 d.

### Factorial experiment

We conducted a fully crossed, three-way factorial experiment to test the independent and joint effects of rainfall (no water vs. water addition), nurse plants (open desert vs. nurse plants) and granivores (no granivore-exclusion cage vs. granivore-exclusion cage) on the germination and initial seedling recruitment of senita cacti. We did not include seed banks in the factorial experiment, as they were not significant factors contributing to recruitment (see Results). Due to the magnitude and extensive replication of this experiment, we were only able to conduct it at Polilla Flats. We selected 18 locations at Polilla Flats, each of which received one plot (30 x 30 cm) of each of the eight treatments of the three-way factorial design. Each of the 144 treatment plots received 150 seeds from the current year's fruit crop. For the rainfall treatment, water was added in early July 2009 to small moats around the plots on a daily basis for 6 d, with an equivalent of 230 mm rainfall per plot, which did not exceed 2 SD of mean annual rainfall. The no water treatment was a true 'no rainfall' effect, as no precipitation occurred prior to the initial census of the experiment (1 wk after the water treatment) in 2009 and very little thereafter. Open desert plots were established away from vegetation in the bare soil; nurse plant plots were placed under the canopy of mesquite (*P. glandulosa*). Granivore exclusion was established using chicken-wire cages of 30 x 30 x 8 cm with a 1.0-cm mesh, secured to the ground with 20-cm nails. We censused for germination and seedling recruitment 7–10 d following the establishment of the experiment in the last week of June 2009, which is sufficient time for seedling germination (Holland & Fleming 1999a). We re-censused each plot in April/May of 2010 and 2011 to assess for continued germination and seedling survival (water was not re-applied). Count data of this experiment had a negative binomial distribution in which variance was higher than the mean. We

analysed the factorial experiment using a generalized linear model for negative binomial data (glm.nb in R). We report the analysis of deviance table of the sequential likelihood ratio tests and the probabilities of significance of the chi-squared tests.

## Results

### Field surveys

#### Nurse plant associations

Spatial associations occurred between juvenile senita cacti and 11 nurse plants: *Atamisquea emarginata* (vomito bush; Capparidaceae), *Atriplex canescens* (fourwing saltbush; Chenopodiaceae), *Encelia farinosa* (brittle bush; Asteraceae), *Hibiscus denudatus* (hibiscus; Malvaceae), *Jatropha cinerea* (limberbush; Euphorbiaceae), *Larrea tridentata* (creosote bush; Zygophyllaceae), *Lycium* sp. (box/desert thorn; Solanaceae), *Maytenus phyllanthoides* (mangle dulce; Celastraceae), *Olneya tesota* (ironwood; Fabaceae), *Prosopis glandulosa* (mesquite; Fabaceae) and *Suaeda nigra* (seepweed; Chenopodiaceae). The modal distance between juvenile senita and each nurse plant was zero for both plant communities, indicating that juvenile senita rou-

tinely occurred under the canopy of nurse plants (Table 1). Median distances between juvenile senita and different nurse plants were <1 m for both plant communities, but were more often zero at Polilla Flats (Table 1). Observed distances between juvenile senita and nurse plants were <1 m for both plant communities, whereas expected distances between the random points and nurse plants were >3 m and often >10 m (Table 1). Observed distances between juvenile senita and nurse plants were statistically shorter than distances between random points and nurse plants for both plant communities (Table 1). This occurred for each species of nurse plant and for all species combined (Table 1).

#### Nurse plant density

Juvenile senita recruitment differed between the two plant communities due at least in part to the densities of nurse plants of each plant community. Senita recruitment was around four times higher at Polilla Flats ( $36.3 \text{ ha}^{-1}$ ) than Seri Flats ( $9.4 \text{ ha}^{-1}$ ), corresponding with a higher density of nurse plants at Polilla Flats ( $38.3 \text{ ha}^{-1}$ ) than Seri Flats ( $9.3 \text{ ha}^{-1}$ ; Table 1). Of the 11 nurse plant species of the

**Table 1.** Nurse plant associations with senita cacti at Seri Flats and Polilla Flats. Median (Med) distance (m) is the observed distance between juvenile senita and nurse plants (modal distances were all zero). Mean  $\pm$  SE (sample size) of observed distances (m) between juvenile senita and nurse plants and of expected distances (m) between random points and nurse plants. All two-sample *t*-values with *df* as a subscript have  $P < 0.0001$ , with the exception of those with an \* which have  $P < 0.005$ . % is the percentage of juvenile senita associated with a particular nurse plant species. Density is the number of individuals per hectare based on random point sampling. Species with '—' were not a component of the flora of that site.

|                   | Site    | Med  | Observed              | Expected               | <i>t</i>          | %    | Density |
|-------------------|---------|------|-----------------------|------------------------|-------------------|------|---------|
| All plants        | Seri    | 0.10 | $0.55 \pm 0.04$ (430) | $10.92 \pm 0.55$ (425) | $t_{428} = -18.8$ | 100  | 9.3     |
|                   | Polilla | 0.00 | $0.07 \pm 0.02$ (261) | $6.46 \pm 0.38$ (276)  | $t_{276} = -16.9$ | 100  | 38.3    |
| <i>Atamisquea</i> | Seri    | 0.25 | $0.66 \pm 0.08$ (141) | $4.11 \pm 0.55$ (55)   | $t_{56} = -6.2$   | 32.8 | 1.2     |
|                   | Polilla | 0.00 | $0.13 \pm 0.13$ (5)   | $11.97 \pm 0.97$ (41)  | $t_{41} = -12.1$  | 1.9  | 5.7     |
| <i>Atriplex</i>   | Seri    | 0.50 | $0.51 \pm 0.16$ (9)   | $12.14 \pm 2.18$ (36)  | $t_{35} = -5.3$   | 2.1  | 0.8     |
|                   | Polilla | 0.20 | $0.52 \pm 0.25$ (12)  | $5.94 \pm 0.87$ (40)   | $t_{44} = -6.0$   | 4.6  | 5.6     |
| <i>Encelia</i>    | Seri    | 0.30 | $0.54 \pm 0.10$ (55)  | $7.66 \pm 1.15$ (54)   | $t_{53} = -6.2$   | 12.8 | 1.2     |
|                   | Polilla | —    | —                     | —                      | —                 | —    | —       |
| <i>Hibiscus</i>   | Seri    | 0.00 | $0.41 \pm 0.15$ (18)  | $17.40 \pm 2.04$ (47)  | $t_{46} = -8.3$   | 4.2  | 1.0     |
|                   | Polilla | —    | —                     | —                      | —                 | —    | —       |
| <i>Jatropha</i>   | Seri    | 0.05 | $0.80 \pm 0.55$ (5)   | $12.42 \pm 1.86$ (28)  | $t_{30} = -6.0$   | 1.2  | 0.6     |
|                   | Polilla | 0.00 | $0.07 \pm 0.07$ (10)  | $7.18 \pm 0.82$ (42)   | $t_{41} = -8.7$   | 3.8  | 5.8     |
| <i>Larrea</i>     | Seri    | 0.80 | $0.90 \pm 0.16$ (27)  | $17.04 \pm 1.69$ (53)  | $t_{52} = -9.5$   | 6.3  | 1.2     |
|                   | Polilla | —    | —                     | —                      | —                 | —    | —       |
| <i>Lycium</i>     | Seri    | 0.00 | $0.44 \pm 0.06$ (123) | $4.59 \pm 0.84$ (55)   | $t_{54} = -4.9$   | 28.6 | 1.2     |
|                   | Polilla | 0.00 | $0.05 \pm 0.04$ (28)  | $3.53 \pm 0.43$ (48)   | $t_{47} = -8.1$   | 10.7 | 6.7     |
| <i>Maytenus</i>   | Seri    | 0.00 | $0.52 \pm 0.17$ (28)  | $12.13 \pm 1.61$ (54)  | $t_{54} = -7.2$   | 6.5  | 1.2     |
|                   | Polilla | 0.00 | $0.10 \pm 0.10$ (3)   | $15.77 \pm 2.93$ (9)   | $t_8 = -5.3^*$    | 1.1  | 1.3     |
| <i>Olneya</i>     | Seri    | —    | —                     | —                      | —                 | —    | —       |
|                   | Polilla | 0.00 | $0.00 \pm 0.00$ (2)   | $16.23 \pm 3.60$ (7)   | $t_6 = -4.5^*$    | 0.8  | 1.0     |
| <i>Prosopis</i>   | Seri    | 0.00 | $0.11 \pm 0.07$ (24)  | $13.67 \pm 1.63$ (43)  | $t_{42} = -8.3$   | 5.6  | 0.9     |
|                   | Polilla | 0.00 | $0.04 \pm 0.01$ (193) | $3.17 \pm 0.59$ (47)   | $t_{46} = -5.3$   | 73.9 | 6.5     |
| <i>Suaeda</i>     | Seri    | —    | —                     | —                      | —                 | —    | —       |
|                   | Polilla | 0.00 | $0.12 \pm 0.08$ (8)   | $4.23 \pm 0.65$ (42)   | $t_{42} = -6.3$   | 3.1  | 5.8     |

two plant communities, only six were associated with juvenile senita in both communities. Five of the six nurse plant species had higher densities, often five-fold higher, at Polilla Flats than Seri Flats (Table 1).

#### Composition of nurse plant community

Senita recruitment also varied between Polilla and Seri sites due to differences in composition of nurse plant species within each plant community (Table 1). At Polilla Flats, 74 and 11% of senita recruitment occurred under *P. glandulosa* and *Lycium* sp., each having a density of  $7.5 \text{ ha}^{-1}$  (Table 1). At Seri Flats, however, *P. glandulosa* had a density of  $<1 \text{ ha}^{-1}$ , accounting for only 5.6% of senita recruitment. With a low density of *P. glandulosa*, senita recruitment increased under *Lycium* sp. at Seri Flats compared to Polilla Flats (29 vs. 11%), despite *Lycium* density being lower at Seri Flats than Polilla Flats ( $1.5 \text{ ha}^{-1}$  vs.  $6.5 \text{ ha}^{-1}$ ). Similarly, *A. emarginata* accounted for 33 and 2% of senita recruitment at Seri Flats and Polilla Flats, respectively, despite its density being five-fold higher at Polilla Flats than Seri Flats (Table 1). With low densities of *P. glandulosa* at Seri Flats, senita recruitment shifted to other nurse plant species at Seri Flats, including *E. farinosa*, *H. denudatus* and *L. tridentata*, which may not otherwise be important (Table 1). Nonetheless, senita recruitment remained lower at Seri Flats than Polilla Flats largely due to the absence of *P. glandulosa*.

#### Seed bank

We found little evidence of senita cactus seed banks under nurse plants, in the open desert or under senita at either of the two plant communities (Table 2). The mode and median number of seeds collected underneath all 11 nurse

plant species was zero, with the exception of *M. phyllanthoides* and *O. tesota*, which had median seed numbers of 1.0 and 2.5. For each nurse plant species, the number of seeds collected from the soil ranged from a minimum of zero to a maximum  $\leq 20$ , with the exception of *Lycium* sp. and *O. tesota*, which had a maximum of 44 and 24, respectively (Table 2). Of the limited number of seeds that were found in the soil, few remained viable. Germination of the seeds was low, and in most cases  $<10\%$ . Only seeds collected under *A. canescens* had high germination (100%), although *A. canescens* represented  $<5\%$  of senita recruitment at either plant community.

#### Factorial experiment

Seedling recruitment was low in each of the 3 yrs of censusing the treatment plots of the three-way factorial experiment testing the independent and joint effects of rainfall, granivores and nurse plants on the germination and seedling recruitment of senita cacti. In the first census of July 2009, germination and seedling recruitment for the entire experiment was  $<2\%$  of the 21 600 seeds added to the 144 treatment plots. In the second census in 2010, following low to nearly absent winter rains, no seedling survival from the prior year and no new seedling recruitment was observed in any of the 144 plots. In the third census of 2011, recruitment was zero. Despite low overall recruitment, multi-factorial conditionality did occur for the independent and joint effects of rainfall, granivores and nurse plants on germination and seedling recruitment in 2009 (Table 3, Fig. 1). There was a significant main effect of rainfall on germination and seedling recruitment. Initial seedling recruitment was significantly higher for the rainfall (water addition) than the no rainfall (no water) plots (Table 3, Fig. 1). In fact, 99.7% (all but one seed) of

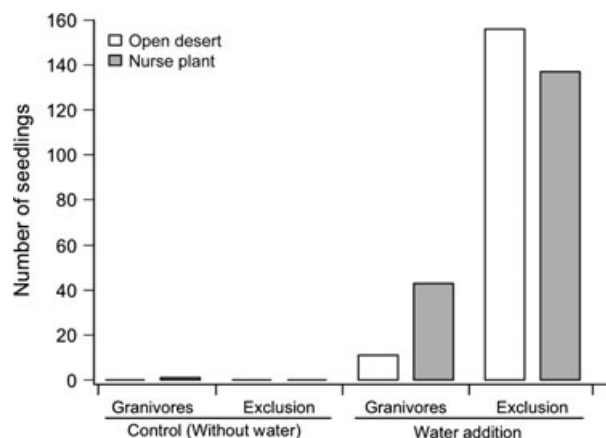
**Table 2.** Mode, median, range and percentage germination (%germ) of columnar cactus seeds recovered from soil samples collected from beneath nurse plants, the open desert and senita cacti (*Pachycereus schottii*) at Seri Flats and Polilla Flats study sites.

|                                | Seri flats |        |       |       | Polilla flats |        |       |       |
|--------------------------------|------------|--------|-------|-------|---------------|--------|-------|-------|
|                                | Mode       | Median | Range | %germ | Mode          | Median | Range | %germ |
| <i>Atamisquea emarginata</i>   | 0          | 0      | 0–16  | 6     | 0             | 0      | 0–20  | 0     |
| <i>Atriplex canescens</i>      | 0          | 0      | 0–14  | 100   | 0             | 0      | 0–2   | 100   |
| <i>Encelia farinosa</i>        | 0          | 0      | 0–1   | 66    | —             | —      | —     | —     |
| <i>Hibiscus denudatus</i>      | 0          | 0      | 0–9   | 8     | —             | —      | —     | —     |
| <i>Jatropha cinerea</i>        | 0          | 0      | 0–1   | 0     | 0             | 0      | 0–0   | —     |
| <i>Larrea tridentata</i>       | 0          | 0      | 0–0   | —     | —             | —      | —     | —     |
| <i>Lycium</i> sp.              | 0          | 0      | 0–0   | —     | 0             | 0      | 0–44  | 0     |
| <i>Maytenus phyllanthoides</i> | 0          | 0      | 0–5   | 33    | 0             | 1      | 0–10  | 0     |
| <i>Olneya tesota</i>           | —          | —      | —     | —     | 0             | 2.5    | 0–24  | 5     |
| <i>Prosopis glandulosa</i>     | 0          | 0      | 0–2   | 0     | 0             | 0      | 0–1   | 0     |
| <i>Suaeda nigra</i>            | —          | —      | —     | —     | 0             | 0      | 0–12  | 25    |
| Open desert                    | 0          | 0      | 0–0   | —     | 0             | 0      | 0–0   | —     |
| <i>Pachycereus schottii</i>    | 0          | 3.5    | 0–16  | 20    | 0             | 4      | 0–16  | 0     |

**Table 3.** Statistics for the three-way factorial experiment assessing the independent and joint effects of rainfall (without and with water addition), open desert vs. nurse plants and granivores (without and with granivore exclusion cage) on germination and seedling recruitment of senita cacti. The analysis of deviance table is for a generalized linear model for negative binomial data with sequential likelihood ratio tests and the probabilities of significance of the chi-squared tests. *df*, degrees of freedom; *Res. df*, residual degrees of freedom; *Res. Dev.*, residual deviance.

|                            | <i>df</i> | Deviance | <i>Res. df</i> | <i>Res. Dev.</i> | <i>P</i> ( $> \chi^2$ ) |
|----------------------------|-----------|----------|----------------|------------------|-------------------------|
| Null                       |           |          | 143            | 315.99           |                         |
| Rainfall                   | 1         | 188.86   | 142            | 127.14           | <b>0.0001</b>           |
| Nurse plant                | 1         | 0.17     | 141            | 126.97           | 0.6850                  |
| Granivore                  | 1         | 33.02    | 140            | 93.96            | <b>0.0001</b>           |
| Rainfall: Nurse            | 1         | 1.01     | 139            | 92.95            | 0.3140                  |
| Rainfall: Granivore        | 1         | 3.75     | 138            | 89.19            | 0.0530*                 |
| Nurse: Granivore           | 1         | 6.02     | 137            | 83.18            | <b>0.0140</b>           |
| Rainfall: Nurse: Granivore | 1         | 0.00     | 136            | 83.18            | 0.9990                  |

\*Note, removing the one germinated seed in the no water/granivore/nurse plant treatment from statistical analyses shifted the *P*-value to 0.99 without changing the significance of any other *P*-value.



**Fig. 1.** Results of the three-way factorial experiment for the effects of rainfall (without and with water addition), open desert vs. nurse plants and granivores (without and with granivore exclusion cage) on the germination and seedling recruitment of senita cacti. Counts of germinating and seedling recruitment are cumulative among replicate plots. Statistical analyses are in Table 3.

germination and seedling recruitment occurred in the water addition treatment. There was also a significant main effect of granivory on germination and seedling recruitment. Initial seedling recruitment was lower in the presence of granivores than when granivores were excluded with cages, for both the open desert and under nurse plant treatments (Table 3, Fig. 1). There was not a significant main effect of nurse plants, indicating that nurse plant facilitation of early seedling recruitment depended on the co-occurrence of other biotic and abiotic factors.

A significant two-way interaction did not occur between rainfall and granivory for germination and initial seedling recruitment, nor did a significant three-way interaction

occur among rainfall, nurse plants and granivory (Table 3, Fig. 1). A significant two-way interaction did occur between granivory and nurse plants ( $P = 0.014$ ; Table 3, Fig. 1). While early seedling recruitment was lower when granivores were present than absent, initial seedling recruitment increased under nurse plants compared to the open desert when granivores were present, but decreased under nurse plants compared to the open desert when granivores were absent. Indeed, the lack of shade could be beneficial with abundant rainfall and absence of granivores (cf. Holmgren et al. 1997). The marginally significant ( $P = 0.053$ ) interaction between rainfall and granivory (Table 3) was due to one seed germinating in the no water, granivore, nurse plant treatment. Removing that one data point shifted the *P*-value to 0.99, but did not alter the significance of any other statistical effect, indicating that the rainfall effect on seedling recruitment did not depend on nurse plants or granivory.

## Discussion

The biotic and abiotic conditions of a local community may act independently or jointly in shaping the facilitative effects of one plant on another in the early establishment of seedlings. In this study, we showed the conditionality and hierarchy of mechanisms contributing to senita cactus recruitment and nurse plant facilitation, including the effects of seed banks, rainfall, granivory and nurse plants. An individual senita cactus can produce thousands of flowers and fruits, and >200 000 viable seeds are routinely produced every flowering season (Holland & Fleming 1999a,b; Holland et al. 2004; Holland & Chamberlain 2007), leading to many millions of seeds entering a population on an annual basis. Hence, senita recruitment dynamics are not likely to be particularly influenced by variation in seed production, as is commonly observed in many other plant species (Harper 1977; Crawley 1997). We found few to no cactus seeds in the very large volumes of soil samples collected from the open desert, under nurse plants or under senita cacti. As soil cores were collected prior to that year's seed production, the very few seeds found represented the totality of the soil seed bank. While cactus seeds may remain viable from months to over a year (Mandujano et al. 1997), our results support the lack of soil seed banks and multi-year seed dormancy in Cactaceae (Rojas-Aréchiga & Vázquez-Yanes 2000; Godínez-Álvarez et al. 2003). Lack of cactus seed banks likely results from seed desiccation, seed decomposition and granivory, along with cactus seeds likely not having evolved prolonged dormancy (Finch-Savage & Leubner-Metzger 2006). Thus, cactus seed banks did not affect senita recruitment, nor did they modulate other mechanisms contributing to recruitment.

To a much greater extent than soil seed density, juvenile senita cacti were consistently associated with 11 different nurse plants between the two plant communities studied in the Sonoran Desert: one degraded of its key nurse plants and the other with its nurse plants intact (Tables 1, 2). Those few studies that have examined nurse plant relationships with senita cacti identified *Bursera microphylla*, *Celtis pallida*, *Lycium andersonii*, *L. berlandieri*, *Olneya tesota* and *Zizyphus obtusifolia* as nurse plants, providing at least shade, and in northern distributions also protection from winter frost (Parker 1989; Suzán et al. 1996; Sosa & Fleming 2002). Density and composition of nurse plant species differed between the plant communities, resulting in reduced senita recruitment and shifts to alternative nurse plant species in the community degraded of its nurse plants compared to the intact plant community. The differences in senita recruitment between the two study populations are attributed to the low density of mesquite at Seri Flats ( $0.9 \text{ ha}^{-1}$ ) vs. Polilla Flats ( $6.5 \text{ ha}^{-1}$ ). Mesquite's low density at Seri Flats is attributed to human population growth of Bahia de Kino and the resulting increase in selective harvesting and overexploitation of mesquite and ironwood for firewood, wood carvings and charcoal as commercial products (Suzán et al. 1994). Historically a small fishing village, Bahia de Kino has expanded from <450 people in 1970 to >6,000 in 2010 (INEGI 2011), including a large expatriate and tourist community. We do not have quantitative data on nurse plant harvesting, but >20 yrs of observations indicate much more harvesting at the closer, more easily accessed Seri Flats than at Polilla Flats, the former having few mesquite and no ironwood (Tables 1, 2; F. Molina-Freaner & J.N. Holland, pers. obs.). Differences in density and composition of nurse plant species between communities can be key factors mediating nurse plant facilitation of cactus recruitment. However, these observations on nurse plant degradation are not replicated, and thus there is also a chance that the results could be due to site effects.

While it is well recognized that plant facilitation can shift to competition along abiotic stress gradients (Holmgren et al. 1997; Callaway 2007; McCluney et al. 2011), the extent of the positive effects of facilitation are conditional upon the biotic and abiotic contexts of a community. Our three-way factorial experiment simultaneously tested the effects of rainfall, granivory and nurse plants on the germination and early seedling recruitment of senita cacti. Despite well-recognized positive effects of nurse plants on cactus recruitment, there was not a significant main factor effect of nurse plants on the germination and seedling recruitment of senita cacti, indicating that nurse plant facilitation of initial stages of cactus recruitment was dependent on other biotic and abiotic factors. The positive effects of nurse plants on germination and initial seedling recruitment depended on rainfall.

Contrary to the lack of a main factor effect of nurse plants, there were significant main factor effects for rainfall and granivory. In the absence of rainfall, germination and seedling recruitment did not occur, indicating that nurse plants may only facilitate cactus recruitment when there is sufficient rainfall. Those seeds that did germinate did not survive the following 2 yrs, likely due to the low to nearly absent precipitation in years following the water treatment, again indicating that nurse plant facilitation of cactus recruitment varies with rainfall in the Sonoran Desert. Likewise, there was a significant main factor effect of granivory. Within the rainfall treatment, early seedling recruitment was higher when granivores were absent than when they were present. Indeed, seeds are an important food resource in arid regions for a variety of consumers, including birds, rodents and ants, whose granivory impedes plant recruitment (Sosa & Fleming 2002; Godínez-Álvarez et al. 2003). In fact, we often saw that nearly all of the 150 seeds were rapidly removed (24–48 h after seed addition) from plots with no granivore cages. Yet, there was a significant two-way interaction between granivory and nurse plants, indicating that the effect of nurse plants on germination and seedling recruitment varied with granivory. When granivores were present, seedling recruitment was higher under nurse plants compared to the open desert, suggesting that nurse plants provide cacti with escape from seed predation. In turn, the interaction between granivory and nurse plants was contingent on rainfall, and it may well also be contingent on seed dispersal to nurse plants vs. the open desert. The seeds that escaped granivory under nurse plants were likely obscured from consumers by detritus under the plants.

Results from the observational studies on nurse plant associations and from the factorial experiment on early seedling recruitment confirm the general role of nurse plants in recruitment of senita cacti in particular. Indeed, we observed almost no survival of juveniles (< 1.2 m) in the absence of nurse plants. Moreover, in the factorial experiment, seedling recruitment was largely limited to nurse plants, except in the case of the open desert when granivores were excluded (Fig. 1). Lack of a significant main factor effect of nurse plants in the factorial experiment was due to interactions with other mitigating variables, including rainfall and granivores. Lack of a main factor effect of nurse plants should not be interpreted as contradictory to the observational results or the well-established role of nurse plants in cactus recruitment. Rather, these results show some of the specific mechanisms and conditions that cause nurse plants to be so influential.

In many, if not most, cases positive effects of facilitation occur through one plant's amelioration of unfavourable biotic or abiotic conditions for another plant. Nurse plant facilitation of cactus recruitment occurs when perennial

shrubs and trees enhance their germination, seedling success and recruitment by providing more favourable shade and light environments, nutrient and water conditions and lower risks of granivory and herbivory (Godínez-Álvarez et al. 2003). Our results show the hierarchical effects shaping seedling recruitment of senita cacti, namely the predominant effects of rainfall in increasing recruitment and of granivory in decreasing recruitment. It is primarily under adequate rainfall conditions that nurse plants play a key role in increasing seedling recruitment and survival. In this way, the long-term population dynamics of senita cacti, as mediated by juvenile recruitment, may be driven more by rainfall, nurse plants and granivory than by variation in seed production resulting from its specialized pollination mutualism with senita moths.

### Acknowledgements

We thank A. Galindo-Escamilla, B. Liliana Guzman, F. Kennedy, J. Martínez, A. Min-Venditti, A. Ramirez Hernandez, M. Rodríguez Galindo, E. Villasenor and A. Waguespack for assistance with field and laboratory work. E. Ezcurra, M. Huston and several anonymous reviewers have aided in the improvement of this manuscript. We thank Prescott College Field Station for continued logistical support. This work has been supported by US National Science Foundation grants DEB-0814523 and DEB-1147630.

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