Nurse Plant Associations in the Chihuahuan Desert Shrublands

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Abstract—Spatial studies in the Chihuahuan Desert of associations with *Larrea* shrub islands found juveniles more often associated with shrub islands than unassociated. The spatial structure of the shrub islands points to Nurse Plant facilitation of seedlings. Experiments tested the effects of canopy, shrub islands, and understory on five perennials' germination. Longer survival times, but not higher germination, of *Zinnia acerosa* were found beneath artificial canopies in intershrub areas and cleared shrub islands as compared to intact shrub islands. Therefore, *Zinnia* may be a poor competitor, preferring germination microsites with few competitors, regardless of Nurse Plant effects.

It is often suggested in arid and semiarid environments, that adult plants facilitate germination and establishment. This idea is commonly called the Nurse Plant Hypothesis (Went 1942; Nabhan 1975; Nobel 1980; McAuliffe 1984a; Carlsson and Callaghan 1991; Cody 1993). Many seedlings in arid and other zones can be found associated either directly under (Nobel 1980) or near the canopy of adult plants (Carlsson and Callaghan 1991; Aguiar and Sala 1992; Belsky 1994). The mechanisms of these associations are often not known, but are usually credited to physical or biotic facilitation provided by the "safe sites" of the Nurse Plant as compared to other microsites (Fowler 1986a, 1986b; Huenneke and Sharitz 1986; Fowler 1988; Scherff and others 1994). These cited physical facilitations include: increased nutrient levels (Vetaas 1992; Belsky 1994), decreased soil temperatures (Nobel 1980), and increased soil moisture (Nobel 1980; Belsky 1994), all compared to areas outside of the Nurse Plant's influence.

On shrub islands in arid zones, the gradients of soil parameters such as carbon, nitrogen, and moisture shift dramatically across centimeters (Charley 1972; Charley and West 1975; Jackson and Caldwell 1993). The microsites provided by these putative Nurse Plants have higher nutrient levels (Vetaas 1992), translating into higher productivity for associated plants (Tiedemann and Klemmedson 1973; 1977; Kellman 1979; Escudero and others 1985; Georgiadis 1989). These nutrient differences are primarily limited to the top of the soil horizon where adult roots are rare (Charley and West 1975; Freckman and Virginia 1989; Franco and others 1994). The Nurse Plant's canopy also has a strong influence on the soil temperature beneath it (Miller and Stoner 1987). Evaporation and transpiration are decreased at lower soil temperatures by the ameliorating effect of the canopy (Tiedemann and Klemmedson 1973, 1977; Nobel 1980; Belsky 1994; Montaña 1994).

At best, though, Nurse Plant relationships are commensalistic for the seedling; at worst the seedlings compete with the adult plant for scarce resources. In arid zones, water stress can be the most limiting factor for plants, especially for seedlings' shallow roots (Leishmann and Westoby 1994). The shallow rooting structures of seedlings compete not only with other seedlings (Eldridge and others 1991; Aguiar and Sala 1994; Leishmann and Westoby 1994), but also with the shallow roots of the adult plant (Tiedemann and Klemmedson 1977; Aguiar and Sala 1992; Belsky 1994).

Larrea dominate creosote (*Larrea tridentata* [D.C.] Cov.) communities in southern New Mexico, complemented by a diverse, spatially associated mix of shrubs, succulents such as prickly pear cacti (*Opuntia* spp.), and annuals. Perennial grasses often sparsely populate large intershrub areas, which have lower soil nutrient moisture levels as compared to the shrub islands (Schlesinger and others 1990). The climate is typical of the Chihuahuan Desert, with irregular spring rains and seasonal storms in the summer (Conley and others 1992).

The spatial structure of the *Larrea* shrub islands points to possible Nurse Plant facilitation of seedlings. To test this possibility, germination trials were conducted under a split-plot design to test the effects of 1) canopies 2) shrub islands and 3) understory on germination. Main factors that influence germination include light, water, and nutrients. Light is generally not considered a limiting factor in the desert, especially under the open canopies of *Larrea*. If the main limitations to germination and establishment are soil temperatures and nutrient levels, then an artificial shrub canopy or increased nutrient loads respectively should stimulate seeds to germinate. However, if the main limitation to germination and establishment is soil moisture, then the absence of other seedlings should increase germination and establishment.

Materials and Methods

Site Description

The experiments were conducted on the New Mexico State University College Ranch near the Jornada Experimental Range, 37 km NNE of Las Cruces, New Mexico. Creosote (*Larrea tridentata* [D.C.] Cov.) and mesquite (*Prosopis glandulosa* Torr.) dominate the shrub community, with a mix of perennial shrubs, subshrubs, cacti, and herbaceous

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annuals making up the rest of the species. The site is on an alluvial wash of the Doña Ana Mountains, with alkaline soils and a shallow calcic horizon (Buffington and Herbel 1965).

Mean summer temperatures approach 40 C (Conley and others 1992), but during the study the June/July mean maximum temperature was near 43 C. Mean precipitation is 218 mm, with the bulk (> 120 mm) coming in strong thunderstorms in July, August and September, that begin July 4th ±14 days (Buffington and Herbel 1965). During the study summer the summer rains began on July 26th and brought 32 mm of rain at the germination site during July and August.

Shrub Island and Intershrub Area Criteria

The *Larrea* shrub islands that were chosen were mature enough to have few shallow roots (>1.5 meters tall) (Franco and others 1994), and at least 2 meters in diameter. Intershrub areas were paired with chosen shrub islands and were at least 4 meters in diameter and had all grass clumps and juvenile perennial plants removed. From the sample, we chose a random sub-sample of 48 intershrub areas and 48 shrub islands. The sample of randomly chosen shrub islands was nearly uniform in size and understory species composition.

Shelters and Seed Cages

Two experiments on seedling germination were conducted. The first experiment was a factorial of four treatments with eight replicates each testing the effects of shrub islands and intershrub areas on germination and establishment. In this factorial, all shrub islands were treated by removing all aboveground shrub and plant biomass on the shrub island. All intershrub areas were treated by removing all grasses and other plants within one meter of the center of the plot. Artificial canopies sheltered half of the shrub islands (SHR-Shade) and intershrub areas (ISA-Shade) while the other two treatments of the factorial were left uncovered (SHR-Open, ISA-Open). To simulate the shrub canopy, these shade canopies were constructed from 1 m^2 60% shade cloth (approximately the shade percentage of adult *Larrea;* V. Gutschick, pers. comm.) and held in place one meter above the plots. A second experiment of two treatments tested the effect of understory on germination. In the first treatment, the shrub canopy was left intact and all understory biomass was removed (No US); the other treatment was left entirely intact and served as the control for shrub islands in both experiments (SHR-Intact).

The experimental unit in both experiments was the seed cage. To test the differences in the microsites, seeds of five species (*Zinnia acerosa* (100 seeds), *Larrea tridentata* (50 seeds), *Prosopis glandulosa* (30 seeds), *Gutierrezia microcephala* (50 seeds), and *Opuntia imbricata* (50 seeds)) were dispersed on July 6th, 1994, in each 100 cm^2 seed cages. *Larrea*, *Prosopis*, and *Opuntia* were all scarified, either by acid or mechanically, before they were placed in plots.

Three major threats exist for seeds in the desert: ants, kangaroo rats, and wind or water movement. To exclude ants, an exclosure of 15 cm garden fencing formed a rectangle of 2000 cm^2 that was centered on the seed cage. The edging was coated with Tree Tanglefoot™, a commercial resin that traps insects. To exclude the kangaroo rats and bird predators, 50 cm high, 1-cm diameter chicken-wire exclosures surrounded the seed cages. Finally, to minimize seed movement due to water or wind, a 1 cm thick layer of common sand was spread over the plot after the seeds were dispersed.

The plots were monitored every three days from July 6th, 1994, until September 12th, 1994, and thereafter sampled every 21 days until early January 1995. A plastic overlay for each replicate allowed the location and survival of each seedling to be recorded. Data from these overlays were then translated into the survival curves for each species.

Microsite resource levels were measured for soil moisture and soil temperature. Soil moisture was measured gravimetrically once a week for 8 weeks from the time the seeds were sown on July 6, 1994 until late August 1994. Ten gram subsamples from the plots were dried until the weight varied less than 0.003 g from day to day. Soil temperature was measured using a thermocouple (Omega II) on six occasions (6 a.m. on July 14th, 1994, 12 p.m. on July 12th, 1994, 4 p.m. on July 6th, 1994, and 8 a.m., 12 p.m., and 4 p.m. on September 20th, 1994). Since the soil was variable across each plot, temperature readings were taken at a depth of 10 cm in the northwest and southeast corners in each plot and then averaged for the plot.

The temperature, moisture, and germination data were then compared with one-way GLM models using repeated measures analysis and contrasts (SAS 1994). Only *Zinnia* germinated, but had a non-normal distribution of germinants (but not survival of germinants). Tukey's transformation (sqrt[n + sqrt(n)]) shifted the data to normality. The analyses used one-way GLM models broken into three comparisons. First, the four treatment factorial was divided into presence/absence of shrub island and presence/absence of an artificial shade canopy and were then compared using repeated measures analyses. A second series of comparisons used one-way comparisons of artificial (ISA-Shade, SHR-Shade) and natural canopies (No US, SHR-Intact) and thirdly, understory (No US) and intact shrub islands (SHR-Intact).

Results

Resource Levels

Mean moisture content varied among treatments with the artificial shade treatments (ISA-Shade and SHR-Shade) having higher values than the naturally shaded treatments (table 1). These artificial shade treatments provided more soil moisture for potential germinants than these other treatments across the whole study. There was no difference in terms of soil moisture between intershrub areas and shrub islands or between artificial canopy and open treatments. Understory plants did increase soil moisture of shrub islands, but not significantly.

Time had a significant effect on soil moisture, most likely due to the lack of rainfall at the site. The only precipitation came during week four when the site received 32 mm of rain. The moisture means for week four show that there were higher levels of soil moisture with artificial shade canopies on week four compared to natural canopies (table 1, fig. 1).

Table 1—The effects of soil moisture on treatment. See text for details on comparison methods.

Time examined		Comparison	df	Mean square	F value	P<F
Entire study		Time	7	0.0441	216.35	0.0001****
		Time	7	0.0441	216.35	0.0001****
		Time*Shade	7	0.0009	4.43	0.0001****
		Time*Shrub	7	0.0001	0.16	0.9924
		Time*Shade*Shrub	7	0.0006	3.31	0.0023***
	Contrast:	Natural canopy/ Artificial canopy	1	0.0087	4.12	0.0435*
	Contrast:	No understory/ Intact shrub isl.	1	0.0018	1.15	0.2847
Week 4 only		Shade	1	0.0128	6.67	0.0155*
		Shrub	1	0.0004	0.28	0.6014
		Shade*Shrub	1	0.0078	4.42	0.0451*
	Contrast:	Natural canopy/ Artificial canopy	1	0.0155	7.38	0.0110*
	Contrast:	No understory/ Intact shrub isl.	1	0.0133	9.08	0.0093**

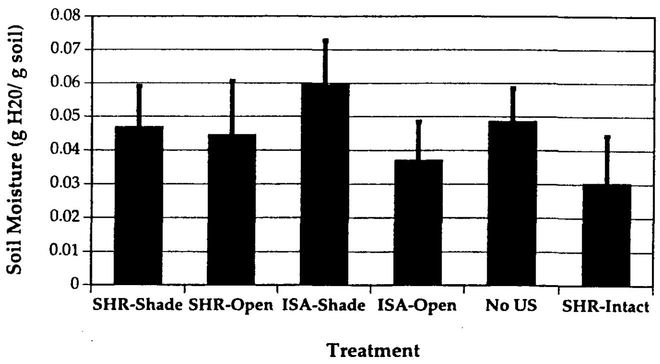

Figure 1—Soil moisture means after 32 mm of rain during the fourth week of the study.

Artificial shade treatments had higher soil moistures than unshaded treatments, but shrub islands were not different than intershrub areas, eliminating any retention effect by the higher levels of organic matter on the shrub islands. The interaction term of shade*shrub was significant, indicating that the combination of shade treatment with the absence of a shrub island (ISA-Shade) resulted in higher soil moisture than SHR-Open (fig. 1). There were positive effects on soil moisture of removing understory biomass, but overall, the artificial canopies produced the strongest effect on moisture levels.

Mean soil temperature did not vary among treatments as natural canopies and artificial canopies were not different, nor were there any effects of the understory on soil temperature (table 2). There were significant differences in soil temperature across time, primarily due to the inclusion of the July afternoon data. There was also an interaction of

Table 2—The effects of treatment on soil temperature. Comparisons follow method described in text.

Time examined		Comparison	df	Mean square	F value	P<F
Entire study		Time	5	42306.920	715.98	0.0001****
		Time*Shade	5	1076.718	18.22	0.0001****
		Time*Shrub	5	26.679	0.45	0.8117
		Time*Shade*Shrub	5	45.502	0.77	0.5726
	Contrast:	Natural canopy/ Artificial canopy	1	78.973	0.35	0.5529
	Contrast:	No understory/ Intact shrub isl.	1	2.870	0.01	0.9127
July afternoon		Shade	1	1278.443	46.59	0.0001****
		Shrub	1	37.719	1.37	0.2513
		Shade*Shrub	1	24.462	0.88	0.3554
	Contrast:	Natural canopy/ Artificial canopy	1	1178.032	40.71	0.0001****
	Contrast:	No understory/ Intact shrub isl.	1	11.390	1.19	0.2943

the artificial canopy treatments and time (shade*time) caused by the artificial canopy treatments were cooler over the whole study. Artificial canopy and open treatment did not differ, nor were there any differences between shrub islands and intershrub areas in terms of soil temperature across the whole study (table 2).

The average mean temperatures of each treatment through the different time periods show no difference except for the 4 p.m. readings in early July (fig. 2). The mean temperatures of the treatments on July 6th at 4 p.m. show higher values for the artificial shade treatments (ISA-Shade and SHR-Shade) as compared to both unshaded and natural canopy treatments (table 2). These two artificial canopy treatments were cooler than the rest of the treatments. The presence of an understory had no effect on soil temperature for shrub islands. Shrub islands were not different from intershrub areas, demonstrating that the results for soil temperature are the same as the results of the moisture data. The presence of an artificial canopy cooled the soil more than a natural canopy did.

Germination Trials

For *Zinnia*, the survival data were normal, but the number of germinants was not normal, so the number of germinants was transformed using Tukey's transformation (fig. 3). The results on the transformed germinant number show no differences (table 3). The Shrub/Shade comparison found an interaction of shrub*shade indicating that shrubs without canopies and intershrub areas with canopies had high germinant numbers. Survival was similar among treatments except for ISA-Shade (table 3, fig. 4). Germinants survived for a longer period of time in intershrub areas than on shrub islands, due primarily to the effects of the artificial canopy. This indicates that the lack of competition from juvenile and adult plants was the most important factor for survival and establishment.

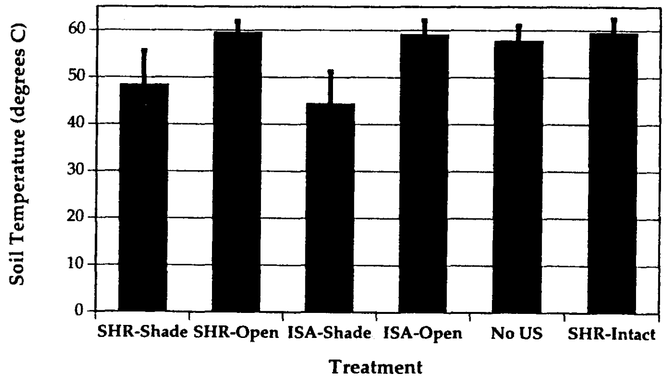

Figure 2—Soil temperature at 4 p.m. in early July. Note differences in shade treatments.

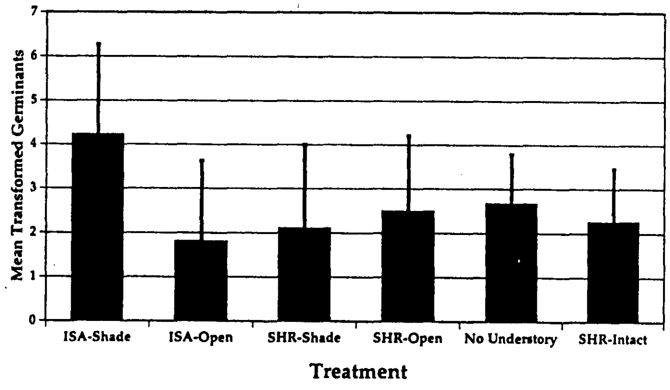

Figure 3—Mean number of germinants for each treatment.

Table 3—The effects of treatment on transformed germinant number and on survival. See text for details on comparison method.

Type		Comparison	Mean square	F value	P<F
Germinants		Shade	4.021	1.16	0.2918
		Shrub	7.934	2.28	0.1426
		Shade*Shrub	15.241	4.38	0.0458*
	Contrasts:	Natural canopy/ Artificial canopy	4.673	0.96	0.3362
	Contrast:	No understory/ Intact shrub isl.	0.676	0.50	0.4931
Survival		Shade	109.243	1.51	0.2847
		Shrub	1171.663	24.35	0.0001****
		Shade*Shrub	268.496	3.71	0.0552
	Contrasts:	Natural canopy/ Artificial canopy	123.617	1.69	0.1946
	Contrast:	No understory/ Intact shrub isl.	7.426	0.33	0.5675

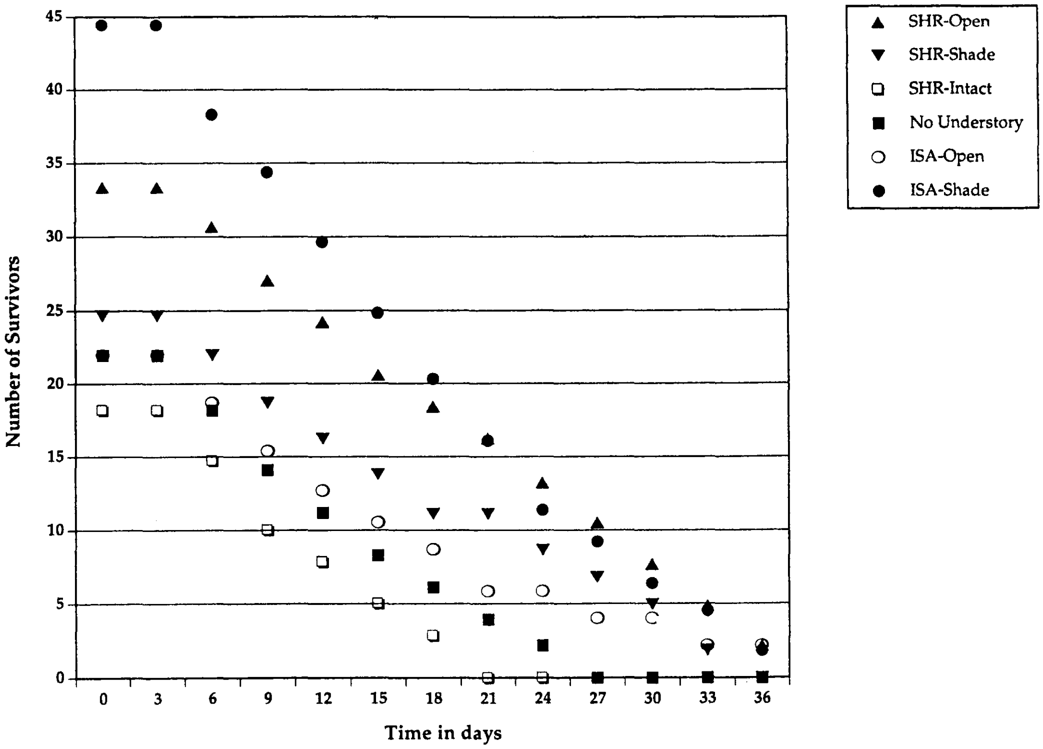

Figure 4—Survivorship curve for *Zinnia* germinants.

Discussion

Microsites and Resources

Subtle environmental differences in light and water strongly influence the germination of seeds in arid environments. Harper and others (1965) suggest that germination and early establishment may have the strictest requirements of all the lifestages of the plant in terms of nutrients and competition. The most important factors affecting soil moisture levels in deserts are root density (Fenner 1985; Franco and Nobel 1988) and soil temperature (Nobel 1984). Microsites that are exposed to direct solar input and those with shallowly rooted plants are less favorable to an arid environment seedling, since increased evaporation lowers soil moisture. Mesquite (*Prosopis*) and creosote (*Larrea*) are both dominant shrubs with strong shrub island associations in many Chihuahuan Desert communities, but both have relatively open canopies, limiting possible Nurse Plant facilitation (Bush and van Auken 1990).

Do Canopies Affect Soil Moisture and Temperature?

The artificial canopy treatments had higher levels of soil moisture compared to shrub canopies, since both ISA-Shade and SHR-Shade had significantly higher soil moisture levels over the whole study compared to the unshaded (ISA-Open and SHR-Open) and the naturally shaded treatments (No US and SHR-Intact). More moisture is available without competition for root uptake and without direct solar input evaporating the upper layers of the soil horizon. Previous work by Schlesinger and others (1990) measured soil moisture differences between *Larrea* shrub islands in intershrub areas and found a similar canopy shading effect on soil moisture. Belsky (1994) suggests that Nurse Plant effects should be more noticeable in more arid environments as the effects of shade on water relations become stronger.

The temperature data suggest that the most significant factor for soil temperature in different microsites could be the quality and density of the canopy shading the soil. For all time periods, both early and late in the summer growing season, the only difference in soil temperatures among treatments came at the daily high temperature early in the season (4 p.m. on July 6th). At this time, the artificial canopy treatments (ISA-Shade and SHR-Shade) were 10-15 C lower compared to the other treatments. This points to the possibility that the artificial canopies provided a different type of shading than did natural canopies. The open *Larrea* canopy permits larger amounts of direct sunlight compared to the more diffuse shadecloth, even at the same 60% total shading. This difference could eliminate comparison with a natural *Larrea* canopy, since the soil would receive alternate periods of direct sun and sharp shadow.

If the artificial canopy treatments provided more canopy shade than did natural ones, this points to a preferred microsite having the most canopy between the soil and the sun in times of peak temperatures. *Larrea* shrub canopies have never been studied for effects on germination, but some argue that *Larrea*'s canopy is too open to provide any substantive Nurse Plant effect on soil temperature. Juvenile columnar cacti in the Sonoran Desert associate with the nurse plant *Hilaria rigida*, a perennial grass which provides a small, dense canopy (Nobel 1980; Franco and Nobel 1988; Cody 1993). The current data support McAuliffe, since the temperatures of the intact shrub (SHR-Intact) are not different than those of the intershrub areas (ISA-Open).

Do Shrub Islands Influence Germination?

There were no significant differences in germinant number among the treatments, but mean survival was lower for shrub islands compared to intershrub areas. In ISA-Shade, *Zinnia* survived longer with the higher moisture levels and lower temperatures than in the conditions of any other treatment. With the data for soil moisture and temperature included, this points to two possibilities: lower moisture and higher temperatures favor *Zinnia* germination or *Zinnia* is a poor competitor and favors more depauperate areas. The data refute the first possibility since none of the summer's germinants survived longer than 36 days in any treatment. As for the second possibility, *Zinnia* is a poor competitor for nutrients and water since ISA-Shade dominate the survival data compared to the shrub island treatments. Last summer, *Zinnia* survived longer in the more resource-limited, depauperate intershrub areas. It is possible that *Zinnia*'s preferred microsite is a young *Larrea* shrub island without a substantial understory. Thus, a *Larrea* shrub island would provide adequate shade for the germinants, lower soil temperatures through shading, but higher soil moistures in the absence of understory competitors.

Are There Nurse Plants in the Chihuahuan Desert?

There have been several studies of nurse plants in deserts of the Southwestern US and Mexico (Nabhan 1975; McAuliffe 1984b; Yeaton and Manzares 1986; Franco and Nobel 1988; Valiente-Banuet and Ezcurra 1991; Cody 1993), but all of them focused on succulents in the Sonoran and Mojave Desert. Shrubs and subshrubs in southern Mexico form shrub islands that structure the community spatially (Silvertown and Wilson 1994). Spatial studies in the Southwest US and Mexico have found that there is a significant focusing of productivity around shrub islands along with a range of interactions, from facilitation (nurse plants) to competitive inhibition (Charley and West 1975; Silvertown and Wilson 1994). Silvertown and Wilson (1994) concluded that *Larrea* served as a "focus shrub" with all other species occurring in association with *Larrea* in the southern Chihuahuan Desert. Other studies in the northern Chihuahuan Desert suggest that there are similar patterns for annuals focusing on *Larrea* and *Prosopis* in shrub communities (Lightfoot 1991).

Our results show a similar pattern of association. These results demonstrate only the shrub islands' effects impacting one species, *Zinnia*, and not surprisingly, suggest that it is a complex mechanism that determines the regeneration niche of that seedling (Grubb 1979). According to spatial studies, *Zinnia* associated with a *Larrea* shrub island more often than chance would allow. However, according to germination and resource data here, *Zinnia* seedlings survived longer in intershrub treatments with higher moisture, lower temperatures, and presumably fewer nutrients. This suggests that *Zinnia*'s survival may depend on a lack of competitors. Thus, the optimal association for establishment of a *Zinnia* is then a *Larrea* shrub island with few understory plants.

The germination study points to a variety of mechanisms that could account for the moisture and temperature data. The most obvious is a physical facilitation of soil factors. It is possible that there was some facilitation of soil factors by shrub islands such as more available moisture that gravimetric methods would not detect. It is also possible that any historic *Larrea* shrub islands' facilitation of *Zinnia* went undetected during the study due to unusual weather. Finally, it is possible that the observed *Zinnia-Larrea* spatial associations represent germination under different soil conditions (for example, higher moisture, lower soil temperatures) and consequent juvenile survival that is not dependent on shrub islands. A more complete picture of species' responses would involve examining the spatial association of *Zinnia* and understory plants around *Larrea* shrub islands during a summer with a more regular rainy season.

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