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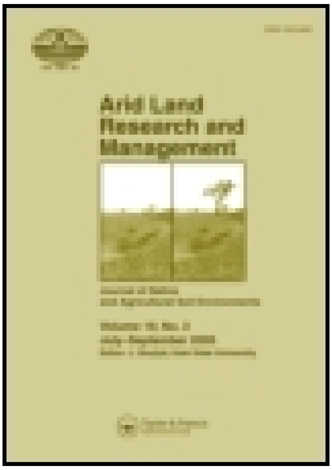

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Assessing Emergence of a Long-Lived Monocarpic Succulent in Disturbed, Arid Environments: Evaluating Abiotic Factors in Effective Agave Restoration by Seed

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Assessing Emergence of a Long-Lived Monocarpic Succulent in Disturbed, Arid Environments: Evaluating Abiotic Factors in Effective Agave Restoration by Seed

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Agave palmeri Engelmann is a semelparous perennial succulent thought to provide a critical food source for the endangered species, *Leptonycteris curasoae* Miller. Concern over impacts to existing *A. palmeri* populations has accelerated interest into reestablishing populations after disturbance. Little is known about its early life history and potential for restoration by seed in its arid habitat. In a greenhouse we measured emergence for 5.5 months across treatments with four variables: simulated precipitation (low: 170 mm, average: 285 mm, high: 390 mm), shade (present, absent), surface mulch (straw, gravel, bare soil), and soil type (sand, sandy loam, loamy sand). The highest emergence was associated with high simulated precipitation (33%), straw mulch (42%), shade (38%), and the loamy soils (mean: 30%). High simulated precipitation on shaded, straw mulched treatments had the highest overall emergence (63%). Lowest emergence involved low simulated precipitation (11%), bare soil (9%), absence of shade (10%), and sandy soil (10%). Low levels of simulated precipitation, combined with unshaded, bare soil treatments—conditions common in heavily disturbed arid environments—had zero seedling emergence. Our results indicate that microsite conditions play a crucial role in the emergence of this species, and manipulation of these conditions may significantly increase emergence, even when water availability is low. This is critical information for land managers attempting to recover populations, as duration and frequency of rainfall are characteristically variable in regions *A. palmeri* inhabits. Thus, the use of surface mulches and shade may effectively facilitate restoration in large-scale disturbances when unfavorable conditions cannot be controlled.

Keywords *Agave palmeri*, arid systems, emergence, *Leptonycteris curasoae*, microsites, restoration, revegetation

Introduction

Agave palmeri Engelmann (Palmer's Agave) occurs in oak woodland and grama grassland communities at elevations between 900 and 1,900 m in southeastern Arizona and southwestern New Mexico, USA, and northern Sonora, MX. This plant

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is thought to provide a critical food source for an endangered species, *Leptonycteris curasoae* Miller (lesser long-nosed bat), a migratory nectar-feeding bat (Schaffer and Schaffer, 1977; Howell and Roth, 1981; Ober and Steidl, 2004; Ober et al., 2005). Habitat loss and degradation due to mining, fire, grazing, and urban development have initiated research efforts to quantify the effects of such impacts on *A. palmeri* populations, but little is known about the restoration potential of this species. Recent studies have suggested that preservation of this agave species and restoration of its populations may be critical factors to *L. curasoae* recovery (Ober and Steidl, 2004; Ober et al., 2005).

Agave palmeri plants grow for up to 35 years before flowering in summer to early fall and then die after producing a single 3–5 m tall inflorescence. Each individual produces tens of thousands of seeds, which shake loose from capsules, raining down over and adjacent to the parent plant. Although little information is available about the life history of *A. palmeri,* this species is thought to rely primarily on sexual reproduction rather than vegetative cloning (Gentry, 1982, personal communication: Wendy Hodgson). Seeds germinate under warm, wet summer conditions and do not appear to have a dormancy period (Freeman, 1975; Jordan and Nobel, 1979).

Unlike mature agave plants, seedlings are particularly vulnerable to environmental conditions and mortality rates are high (Gentry, 1972; Nobel, 1977) with high surface temperatures and lack of available water suggested as primary causes of seedling mortality during the first year of growth (Jordan and Nobel, 1979, 1982). As has been observed with other desert succulents (Turner et al., 1966; Pierson and Turner, 1998), successful establishment episodes in agave populations may be very infrequent, requiring multiple, consecutive years of favorable conditions to both germinate and establish (Nobel, 1977; Jordan and Nobel, 1979).

Young agave plants are thought to benefit from and possibly require facilitative "nurse" relationships, which may increase moisture and nutrient availability and protect from extreme temperatures, herbivory, and trampling (Turner et al., 1966; Jordan and Nobel, 1979; Peters et al., 2008). Heterogeneous conditions on the soil surface may provide protective microsites for seed germination and emergence, ameliorating temperature extremes, and decreasing evaporative water loss (Steenbergh and Lowe, 1969; Jalota and Prihar, 1998; Post et al., 2004; Li et al., 2005). Soil color, texture, and coarse particle content may impact surface temperatures and influence permeability of the soil profile for root and water infiltration (Martre et al., 2002).

Increasing concern regarding impacted *A. palmeri* populations has led land managers to prioritize investigating its restoration potential. Seed broadcasting is a common revegetation method used in large-scale disturbances with lower costs and other advantages (e.g., Rowe, 2010), however, little is known about factors associated with favorable emergence and survival of *A. palmeri* seedlings. We conducted an experiment to assess the relative importance of four primary environmental variables on *A. palmeri* emergence: precipitation, shade, surface mulch, and soil type. Within our experiment, high levels of simulated precipitation and the presence of shade were expected to have a strongly positive effect on emergence and survival. Mulches were thought to have the potential to create protected microsites for seeds and seedlings and promote increased emergence over bare soil treatments. *A. palmeri* is commonly found on sandy or gravelly soils, thus soil texture was also expected to be an important consideration. Our results attempt to assess the quantitative impact and relative importance of these variables and the potential to prioritize their use in effective restoration of the species in large-scale disturbances.

Methods

In fall 2009, we conducted a greenhouse experiment to assess the potential of restoring *A. palmeri* populations by seed on a reference site in the northeastern Santa Rita Mountains, AZ, U.S.A. (31°50′N, 110°45′W, 1470-1685 m asl). A 2008 survey effort estimated the abundance of *A. palmeri* on the project site as 140 plants/ha (±19 SE) suggesting a relatively dense population (WestLand Resources, Inc., 2009). Conditions from this reference site were simulated in a greenhouse, where we tested the effects of four primary variables on seed emergence and mortality. Treatments included: 1) three simulated precipitation levels calculated from reference site records to replicate typical high, average, and low summer precipitation; 2) one component of a facilitative nurse relationship: shade; 3) three soil surface heterogeneity treatments: straw mulch, gravel mulch, and bare soil; and 4) three soil types common to and collected from the reference site: sand, sandy loam, and loamy sand.

Seed Collection

In October 2008, ripe, present-season seed capsules were collected from 26 *A. palmeri* individuals (hereafter parents) that were at least 40 m apart and occurred across a 300 ha area located at the reference site.

Growth Chamber Trials

Although many other agave species have been tested for emergence response to light sensitivity (Nobel, 1977, 1988; Freeman, 1975), little is known about the affect of light on *A. palmeri* emergence. In order to ensure experimental treatments were not confounded, we tested for light sensitivity using methods outlined by Freeman (1975). Four randomly selected parents were included in the trial. Five seeds from each parent were used per Petri dish in three replicate dishes. Light-limited treatments were sealed in #2 paper bags. Dishes were placed in a lighted growth chamber (550 μmol m^2s^{-1} PAR) at 25°C. This temperature has been shown to be most favorable to germination in other agaves from similar habitats (Freeman, 1975; Nobel, 1988). Germination (defined as a visible radical) was determined after 21 days.

Seed germination among all 26 parents was tested using the maximum number of seeds available from fall collections (2,070 seeds) in a growth chamber simulating summer monsoon conditions typical at the reference site (temperature: 15–37°C; relative humidity: 7–96%; light: up to 550 μmol m^2s^{-1}, mimicking diurnal changes in light intensity at the reference site for a 14-hour day). Ten seeds from each individual were placed on a moistened paper towel, sealed in plastic bags, and randomly placed in the growth chamber. Four replications of each parent were placed in each of two separate trials, for a total of eight replications per parent. Each trial lasted 21 days and concluded with an inventory of germination.

Greenhouse Experiment

The greenhouse experiment took place from August 2009 to February 2010, in an evaporatively-cooled greenhouse at the University of Arizona Campus Agricultural Center, Tucson, AZ, USA. There were four primary variables assessed: simulated precipitation (high, average, low), shade (present, absent), surface mulch (straw, gravel, bare soil), and soil type (sand, sandy loam, loamy sand). Fifty-four distinct treatments were tested (3 × 2 × 3 × 3) with five replications in a full factorial randomized complete block design with blocks arranged along the length of the greenhouse to accommodate varying temperature and humidity relative to the cooling system at opposite ends of the building. A total of 270 15 L plastic nursery pots were used.

A relatively wet summer season was simulated between 15 August and 17 November 2009, with a maximum temperature of 35°C. From 18 November 2009 to 2 February 2010, a dry, cooler autumn period was simulated with lower temperatures (maximum 29°C).

Precipitation treatments were created using reference site records, and were intended to apply amounts that would be expected in low, average, and high summer seasons. From 31 years of data (1976–2006), the median annual precipitation year represented the "average" level (285 mm), and the fourth and twenty-eighth ranks became the "low" and "high" levels, respectively (170 mm and 390 mm). In the wet "summer" season, pots were watered every three days using a downspray sprinkler (one per pot) (DripWorks, Willits, CA, USA) for 94 days, and in the dry "autumn" season no water was applied for 82 days before the final inventory. Three soil types common to the reference site and representing a range of textures (Table 1), were collected at the site from a depth of up to 3 m in an effort to simulate disturbed conditions. Soil was sifted to exclude cobbles greater than 5 × 5 cm and filled to 7 cm below the pot rim. Soil and precipitation treatments match those described by Fehmi and Kong (2012) where more detail can be found.

The shade treatment incorporated a circular wire frame 25 cm above the soil surface and 8 cm above the top of the downspray sprinkler. Frames were covered with knitted polyethelyne sun screen fabric that eliminated 75% of the available light (Easy Gardener, Waco, TX, USA). The fabric draped over the east and west sides, eliminating any direct morning and evening sunlight from reaching the soil surface and leaving the north and south sides open to airflow to minimize dramatic differences in humidity associated with the shade cloth. The unshaded treatment did not have a frame or fabric cover.

The three surface treatments included straw, gravel, and bare soil. In all surface types seeds were deposited directly on the soil surface. In the straw treatment, 34 g (equal to a rate of 2,000 kg per acre) of chopped (<7 cm in length) certified weed-free

Table 1. Characteristics of soils used in the experiment collected from the northeastern Santa Rita Mountain Range, Pima County, Arizona

Soil Type	Texture (%)				Classification	pH	NO_3 (ppm)	PO_4 (ppm)	K (ppm)
	Sand	*Silt*	*Clay*	*Gravel**					
Sand	88	8	4	81	sand	7.1	1	4	64
Sandy loam	68	18	14	43	sandy loam	8.2	2	6	65
Loamy sand	76	18	6	57	loamy sand	8.4	2	3	135

*Gravel size in analysis was 2–50 mm.

straw was applied per pot, based on industry standards (Jalota and Prihar, 1998). For the gravel treatment, 60% of the soil surface was covered with two sizes of red gravel: 67% large sizes (>2 × 4 cm) and 33% small sizes (<2 × 4 cm). The size and density of gravel mulch was determined using photos of soil surfaces adjacent to agaves at the reference site. In the bare soil treatment, no mulch was added to the soil surface.

Data Collection and Environmental Measurements

Ten parents were randomly selected from the 26-parents available, and one seed from each was planted per pot (experimental unit) for a total of ten seeds per pot (270 pots total). Planting locations (10 equally-sized wedges) were randomized for each parent in each pot and seeds were tracked by parent. During the simulated summer rainy period, pots were inventoried every 2–3 weeks and autumn inventories occurred monthly. A seedling was considered emerged if its cotyledon was clearly visible.

Soil volumetric water content (VWC) was measured in every pot on 14 November 2009, approximately 24 hours after irrigating, using a Field Scout TDR 100 soil moisture meter (Spectrum Technologies, Inc., Plainfield, IL, USA). Temperature and relative humidity were measured every 15 minutes in one pot for each of the 18-treatment combinations for the sandy loam soil type, from 12 September to 2 February 2009, using Onset Hobo data loggers (model U23-002, Onset Corporation, Pocasset, MA, USA). Data logger locations were selected randomly from the center of the greenhouse and were attached to the base of the downspray sprinkler, approximately 5 cm above the soil surface.

To compare greenhouse and field temperature and humidity conditions, six Onset Hobo data loggers were set up within 10 cm of young agaves at the reference site, from 19 September 2009 to 2 February 2010. Plants were selected arbitrarily based on size (<10 cm) and number of leaves (≤4), as it was impossible to determine age conclusively. Half of the plants selected were growing in deep shade (>75% mid-day canopy cover), and half of the plants were in the open on exposed, grassy knolls. Sensors were placed 5 cm above the soil surface and measurements were collected every 15 minutes.

Analysis

An ANOVA was used to assess the photosensitivity of *A. palmeri* seeds in the growth chamber trial, using number of seeds germinated as the response variable, and parent, repetition, growth chamber shelf (top or bottom), and treatment (light or dark) as explanatory variables. Summary statistics were used to assess differences in parent germination. Parents were ranked by total number emerged in both growth chamber and greenhouse experiments, and a Spearman's rank correlation coefficient was calculated for results between experimental conditions.

In the greenhouse, percent emergence and survivorship were calculated for each pot. Data were arc-sine transformed to generate a tighter normal quantile plot. To confirm the appropriateness of the data transformation, heterogeneity of variance was tested using a Brown-Forsythe test (Brown and Forsythe, 1974).

A full-factorial mixed-model ANOVA was run for both emergence and survivorship with simulated precipitation, shade, surface mulch, and soil type as explanatory variables. Replication was treated as a random effect. Insignificant variables were eliminated from the full model and the resulting parsimonious model best represents the contribution of the remaining variables (Montgomery, 1984; Venables and Ripley, 1994). Multiple means were compared between treatments using Tukey's HSD tests, except for main shade effects where *t*-tests were used.

A multiple-factor ANOVA was run to assess the differences in volumetric water content between treatments. Weekly means for 4.5 months of temperature and relative humidity data were compared between field and greenhouse data loggers.

JMP software (version 8.0; SAS Institute Inc., Cary, NC, U.S.A.) was used for all statistical analyses. Probability values for significance were set at $p \leq 0.05$ throughout. Experimental design is balanced and least squares means were reported.

Results

Growth Chamber Trials

No significant differences were found between the light (38% germination) and light-limited (45% germination) treatments. In the germination trials, 44% of *A. palmeri* seeds (910 of 2070) germinated over the course of two, 21-day trials. Per parent, total germination ranged between 8–78%, with a majority (65%) of parents ranging between 30%–60% germination.

Greenhouse Experiment

In total, 28% of *A. palmeri* seeds emerged (754 of 2700 seeds) over the 171-day experiment. Over the same period, 36 seedlings (4.8%) died after emergence. Seedling deaths occurred in 33 pots (out of 270) and in 22 unique treatments (out of 54). No trends were identified between seedling mortality and experimental treatments. Significance tests on seedling survivorship were virtually identical to those of seedling emergence with means varying no more than 4%, and thus results for survivorship are not reported here.

Each of the four main effects and three interacting treatments were significantly associated with seedling emergence ($R^2 = 0.77$). In simulated precipitation treatments (Table 2), high, average, and low levels each differed significantly; high levels were associated with about 3 times more mean emergence than low levels. Shaded treatments (Table 2) were associated with more than 3 times the seedling emergence of unshaded treatments. Each of the three surface treatments (Table 2) exhibited significantly different mean seedling emergence; straw was associated with about double the emergence of gravel and five times that of bare soil. In soil treatments (Table 2), the loamy sand and the sandy loam had similar seedling emergence, and both had about 3 times more emergence than the sand treatments.

High and average simulated precipitation coupled with sandy loam and loamy sand soils had significantly higher mean seedling emergence (averaging 41%) than low precipitation treatments on these soils and on sand treatments across all simulated precipitation levels (averaging 11%) (Table 3).

Mulched sandy loam and loamy sand soils were associated with the most seedling emergence, particularly when coupled with straw mulch (Table 4). Although overall emergence on the sand treatment was low, straw mulch had a similarly positive effect on this soil type, increasing total emergence over that of bare soil. Bare soil treatments of all soil types had the least seedling emergence.

Table 2. Least square means (±SE) for total *A. palmeri* seedling emergence associated with main effect treatments in the experiment from 15 August 2009 to 2 February 2010

Treatment grouping	Treatment	Total mean emergence (%)*
Simulated precipitation	high	32.9 ± 1.16^{a}
	average	26.9 ± 1.16^{b}
	low	10.8 ± 1.16^{c}
Shade	shade	38.0 ± 0.98^{a}
	no shade	10.4 ± 0.98^{b}
Surface	straw	42.1 ± 1.16^{a}
	gravel	21.5 ± 1.16^{b}
	bare soil	8.8 ± 1.16^{c}
Soil type	Loamy sand	30.9 ± 1.16^{a}
	Sandy loam	29.6 ± 1.16^{a}
	Sand	10.3 ± 1.16^{b}

*Means followed by different letters indicate a significant difference ($p \leq 0.05$) within like treatment groupings, based on Tukey's HSD tests and Student's t-test (shade effect only).

Shaded, straw mulch treatments had the highest emergence, even across low simulated precipitation levels (Table 5). The lowest emergence observed in the experiment occurred in average and low simulated precipitation levels across unshaded, bare soil treatment combinations.

Environmental Variables

Volumetric water content between treatments was significantly influenced by three main effects: simulated precipitation, shade, and soil type ($R^2 = 0.87$). High and

Table 3. Least square means (±SE) for total *A. palmeri* seedling emergence associated with simulated precipitation level X soil type treatment interaction in experiment from 15 August 2009 to 2 February 2010

Treatments		Total mean emergence (%)*
Simulated precipitation	*Soil type*	
high	Loamy sand	47.0 ± 1.92^{a}
High	Sandy loam	43.4 ± 1.92^{a}
Average	Loamy sand	37.0 ± 1.92^{a}
Average	Sandy loam	35.3 ± 1.92^{a}
Low	Sandy loam	13.1 ± 1.92^{b}
Low	Loamy sand	12.1 ± 1.92^{b}
High	Sand	12.0 ± 1.92^{b}
Average	Sand	11.4 ± 1.92^{b}
Low	Sand	7.7 ± 1.92^{b}

*Means followed by different letters indicate a significant difference ($p \leq 0.05$) based on Tukey's HSD test.

Table 4. Least square means (±SE) for total *A. palmeri* seedling emergence associated with surface X soil type treatment interaction in experiment from 15 August 2009 to 2 February 2010

Treatments		Total mean emergence (%)*
Surface	*Soil type*	
Straw	Loamy sand	59.5 ± 1.92^{a}
Straw	Sandy loam	55.9 ± 1.92^{a}
Gravel	Loamy sand	25.5 ± 1.92^{b}
Gravel	Sandy loam	24.5 ± 1.92^{b}
Gravel	Sand	$15.0 \pm 1.92^{b,c}$
Straw	Sand	$14.4 \pm 1.92^{b,c}$
Bare soil	Sandy loam	12.5 ± 1.92^{c}
Bare soil	Loamy sand	12.0 ± 1.92^{c}
Bare soil	Sand	3.5 ± 1.92^{d}

*Means followed by different letters indicate a significant difference ($p \leq 0.05$) based on Tukey's HSD test.

Table 5. Least square means (±SE) for total *A. palmeri* seedling emergence associated with simulated precipitation X shade X surface treatment interaction in experiment from 15 August 2009 to 2 February 2010

Treatments			Total mean emergence (%)*
Simulated precipitation	*Shade*	*Surface*	
High	shade	straw	62.8 ± 2.68^{a}
Average	shade	straw	$59.4 \pm 2.68^{a,b}$
High	shade	gravel	$49.2 \pm 2.68^{a,b,c}$
Low	shade	straw	$45.2 \pm 2.68^{a,b,c}$
Average	no shade	straw	$43.0 \pm 2.68^{a,b,c}$
Average	shade	gravel	$39.2 \pm 2.68^{b,c}$
High	shade	bare soil	$38.1 \pm 2.68^{b,c}$
High	no shade	straw	$38.0 \pm 2.68^{b,c}$
Low	shade	gravel	$32.1 \pm 2.68^{c,d}$
Average	shade	bare soil	$30.7 \pm 2.68^{c,d}$
High	no shade	gravel	$17.0 \pm 2.68^{d,e}$
Low	no shade	straw	$9.7 \pm 2.68^{e,f}$
Average	no shade	gravel	$8.2 \pm 2.68^{e,f,g}$
High	no shade	bare soil	$4.9 \pm 2.68^{e,f,g}$
Low	shade	bare soil	$1.7 \pm 2.68^{f,g}$
Low	no shade	gravel	$1.2 \pm 2.68^{f,g}$
Average	no shade	bare soil	$0.7 \pm 2.68^{f,g}$
Low	no shade	bare soil	$0^{\dagger g}$

*Means followed by different letters indicate significant differences ($p \leq 0.05$) based on Tukey's HSD test.

†No seedlings emerged in this treatment combination.

average simulated precipitation were almost equal in VWC (42.1% ± 0.72, 42.0% ± 0.72; mean ± SE), and significantly higher than the low simulated precipitation (31.4% ± 0.72). Shaded treatments were significantly higher than unshaded treatments (39.6% ± 0.65 vs. 37.3% ± 0.65). Each soil type (sandy loam, loamy sand, and sand) had a significantly different VWC (60.1% ± 0.72, 42.9% ± 0.72, and 15.5% ± 0.72, respectively). Three interacting treatments were also significant. In the simulated precipitation x soil type interaction, sand soil of all simulated precipitation levels (14%–17% ± 0.001) was significantly lower in VWC than the loamy soils (48%–67% ± 0.001). The simulated precipitation x surface mulch interaction had high and average levels of simulated precipitation across all surface types (39.8%–45.3% ± 0.001) significantly greater in VWC than low levels (24.8%–38.0% ± 0.001). Finally, simulated precipitation x surface mulch x soil type had loamy soils (34.9%–70.6% ± 0.001) generally with significantly higher VWC than sand soil (12.1%–19.6% ± 0.001), especially with high and average simulated precipitation levels.

Weekly mean greenhouse temperatures (14°C–29°C) were consistently higher than field temperatures (5°C–23°C) over the 20-week monitoring period. Overall, differences in temperature in the greenhouse varied between 5°C–14°C greater than in the field, on a weekly basis. Relative humidity weekly means also appeared to be less variable in the greenhouse (33%–68%) than in the field (23%–80%). In the summer wet period, relative humidity was consistently higher in the greenhouse, with weekly means ranging from 4%–39% higher. Relative humidity in the winter dry period was more often higher in the field, and weekly means were 2%–18% higher than greenhouse means. The greatest relative humidity differences were observed in the first two weeks of the monitoring period, with up to 39% greater RH in the greenhouse.

Parent Effect

Of the 10 parents included in both studies, the range in differences in mean germination/emergence among parents was larger in the growth chamber (8%–78%) than in the greenhouse (6%–42%). Few patterns in individual parent viability were revealed between experiments, with the exception of two individuals, exhibiting consistently the lowest emergence. We found no relationship between parent emergence in growth chamber and greenhouse experiments ($r_S = 0.41$, $n = 10$) [significance threshold: $r_S = 0.63$ ($\alpha = 0.05$); Snedecor, 1956].

Discussion

It is widely acknowledged that agave seedlings are rarely observed in the wild. After a lifetime of observing *Agave* taxa across the Americas, Gentry (1972) claimed he had never seen a seedling less than one year old. Nobel's (1977) research on *A. deserti* estimated that only one in 1.2 million seeds survive to maturity, suggesting that adequate water availability drives germination and establishment "events" to occur infrequently, on the order of one in seventeen years (Jordan and Nobe, 1979; Nobel, 1988).

Our results similarly indicate a strong link between water availability and *A. palmeri* emergence, as high simulated precipitation treatments were associated with 1.2 times more emergence than average levels, and more than 3 times the emergence of low level treatments. However, soil type, surface mulches, and shade appeared to play critical roles in seed response during the early life history of *A. palmeri* and may serve to mitigate for unreliable water availability. Seasonal and inter-annual rainfall patterns are characteristically variable in the regions *A. palmeri* inhabits, thus, mitigating for low water availability may be crucial to establishing *A. palmeri* by seed in disturbed landscapes.

At the reference site the dark red, extremely gravelly sand soil type supports a large population of *A. palmeri*. Contrastingly, in the disturbed conditions of our experiment, it was associated with the lowest emergence levels of all the soil types across most of the treatments. However, consistent across all treatments, *A. palmeri* seeds responded favorably to protected microsite conditions in the form of shade and surface mulches, across all simulated precipitation treatments and all soil types. When mulched with straw or gravel, the sand soil type had significantly higher emergence levels than when left unmulched (over 4 times greater emergence observed). This is particularly notable when considering that all levels of simulated precipitation treatments on the sand soil type were significantly lower in volumetric water content than the other soil types, with high simulated precipitation treatments on the sand soil type 2–3 times lower in volumetric water content than the low simulated precipitation treatments on the other soil types.

Work by Franco and Nobel (1988, 1989) on the facilitative association between the bunchgrass *Hilaria rigida* Thurber and the hosted species *A. deserti* and *Ferocactus acanthodes* (Lemair) Britt. and Rose, found that one of the primary benefits for seedlings associated with the bunchgrass was decreased soil temperatures, even though competition with the nurse plant for water and PAR negatively affected their growth. Straw mulch may be acting similarly by decreasing soil temperatures, minimizing evaporative water loss, and increasing relative humidity, but without competition for resources. Straw has been shown in other studies to significantly reduce temperatures at the soil surface (Jalota and Prihar, 1998). Surface gravel, common at the reference site, was associated with more than double the emergence in our bare soil treatments. In a study by Li et al. (2005), gravel of the size used in this experiment was found to effectively intercept precipitation and retain moisture in the underlying soil, thus increasing the potential to facilitate emergence and establishment at low simulated precipitation levels. Additionally, it is possible that gravel would create heterogeneous texture on the soil surface, maintaining favorable microsites for seed emergence with temporary shade, potentially cooler temperatures, and retarded evaporative water loss (Post et al., 2004; Peters et al., 2008).

The presence of shade also appeared to be relatively consistent in promoting emergence across treatments. Irrespective of simulated precipitation levels, treatments coupled with shade had significantly higher emergence than unshaded treatments, especially when combined with surface mulches. High and average simulated precipitation levels when coupled with shade and straw mulch had an average of 61% associated emergence—the highest levels observed in the experiment. In contrast, low simulated precipitation, coupled with unshaded bare soil treatments (conditions likely in a large-scale disturbance) was the only treatment combination with no emergence observed. Research by Turner et al. (1966) found that unshaded saguaro (*Carnegiea gigantea*) seedlings had significantly higher rates of mortality than shaded seedlings regardless of water availability, and concluded that temperature plays an integral role in limiting the germination and seedling establishment of succulent species in arid environments. Studies on other agave species have offered similar conclusions, suggesting that seedlings are much more sensitive to soil and air temperature extremes than older plants, and that temperature tolerance increases as plant volume and height increase (Nobel, 1984, 1988; Franco and Nobel, 1988).

Restoring *A. palmeri* by seed in conditions common to large-scale disturbances of arid habitat (including exposed soils, lack of protective cover sites, and variable water availability) can be expected to result in very low seed emergence. However, the potential for meaningful landscape-scale restoration of *A. palmeri* by seed appears to be possible if protected microsites facilitating temperature mitigation and water retention are present. The use of shade and mulches, through natural features such as cobbles or boulders, transplanted or reestablished vegetation (especially larger *A. palmeri* plants), and organic debris, or through fabricated shade structures may substantively increase the emergence of *A. palmeri* seeds in disturbed landscapes—even on less favorable substrates and in low water situations. Other factors known to threaten the survivorship of young plants in the wild (such as herbivory and long-term variability in temperature extremes and water availability) still need to be tested. A particular concern in any restoration scenario involving *A. palmeri* should be providing long-term, uninterrupted annual foraging opportunities for *L. curasoae* within impacted habitat. This would require a population with a spectrum of age classes, rather than a single-aged cohort resulting from a seeding effort. Thus, an integrated approach combining seeding, transplants, and conservation of intact populations will be required for developing a truly effective restoration plan for this long-lived species.

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References

Brown, M., and A. Forsythe. 1974. Robust tests for equality of variances. *Journal of the American Statistical Association* 69: 364–367.

Fehmi, J., and T. Kong. 2012. Effects of soil type, rainfall, straw mulch, and fertilizer on semi-arid vegetation establishment, growth and diversity. *Ecological Engineering* 44: 70–77.

Franco, A., and P. Nobel. 1988. Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. *Ecology* 69: 1731–1740.

Franco, A., and P. Nobel. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* 77: 870–886.

Freeman, C. 1975. Germination responses of a New Mexico population of Parry agave (*Agave parryi* Engelm). *The Southwestern Naturalist* 20: 69–74.

Gentry, H. 1972. *The agave family in Sonora*, Handbook #399. United States Department of Agriculture, Washington, D.C.

Gentry, H. 1982. *Agaves of continental North America*. University of Arizona Press, Tucson, Arizona.

Hodgson, W. 2008. Desert Botanical Garden. Phoenix, Arizona. Personal communication.

Howell, D., and B. Roth. 1981. Sexual reproduction in agaves: the benefits of bats; the cost of semelparous advertising. *Ecology* 62: 1–7.

Jalota, S., and S. Prihar. 1998. *Reducing soil water evaporation with tillage and straw mulching*. Iowa State University Press, Ames, Iowa.

Jordan, P., and P. Nobel. 1979. Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the northwestern Sonoran Desert. *American Journal of Botany* 66: 1079–1084.

Jordan, P., and P. Nobel. 1982. Height distributions of two species of cacti in relation to rainfall, seedling establishment, and growth. *Botanical Gazette* 143: 511–517.

Li, X., P. Shi, L. Liu, S. Gao, X. Wang, and L. Cheng. 2005. Influence of pebble size and cover on rainfall interception by gravel mulch. *Journal of Hydrology* 312: 70–78.

Martre, P., G. North, E. Bobich, and P. Nobel. 2002. Root deployment and shoot growth for two desert species in response to soil rockiness. *American Journal of Botany* 89: 1933–1939.

Montgomery, D. 1984. *Design and analysis of experiments*. John Wiley & Sons, New York.

Nobel, P. 1977. Water relations of flowering *Agave deserti*. *Botanical Gazette* 138: 1–6.

Nobel, P. 1984. Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia* 62: 310–317.

Nobel, P. 1988. *Environmental biology of agaves and cacti*. Cambridge University Press, Cambridge, United Kingdom.

Ober, H., and R. Steidl. 2004. Foraging rates of *Leptonycteris curasoae* vary with characteristics of *Agave palmeri*. *The Southwestern Naturalist* 49: 68–74.

Ober, H., R. Steidl, and V. Dalton. 2005. Resource and spatial-use patterns of an endangered vertebrae pollinator, the lesser long-nosed bat. *Journal of Wildlife Management* 69: 1615–1622.

Peters, E., C. Martorell, and E. Ezcurra. 2008. Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (Mammillaria) in the Tehuacán valley, Mexico. *Journal of Arid Environments* 72: 593–601.

Pierson, E., and R. Turner. 1998. An 85-year study of saguaro (*Carnegiea gigantea*) demography. *Ecology* 79: 2676–2693.

Post, D., A. Matthias, A. Batchily, H. Hosler, and R. Huebner. 2004. Effect of organic and rock mulches on the moisture and temperature of Arizona soils. *Journal of the Arizona-Nevada Academy of Science* 36: 111–119.

Rowe, H. 2010. Tricks of the trade: Techniques and opinions from 38 experts in tallgrass prairie restoration. *Restoration Ecology* 18: 253–262.

Schaffer, W., and M. Schaffer. 1977. The reproductive biology of Agavaceae: I. Pollen and nectar production in four Arizona agaves. *The Southwestern Naturalist* 22: 157–167.

Snedecor, G. 1956. *Statistical methods*, 5th ed. Iowa State University Press, Ames, Iowa.

Steenbergh, W., and C. Lowe. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology* 50: 825–834.

Turner, R., S. Alcorn, G. Olin, and J. Booth. 1966. The influence of shade, soil, and water on saguaro seedling establishment. *Botanical Gazette* 127: 95–102.

Venables, W., and B. Ripley. 1994. *Modern applied statistics with S-Plus*. Springer-Verlag, New York.

WestLand Resources, Inc. 2009. Agave survey of the Rosemont holdings and vicinity (unpublished report). Tucson, Arizona. http://www.rosemontcopper.com/assets/docs/reports_10-8-10/biological_information/agave/agave_survey_tech_memo_031109.pdf. Accessed July 2009.