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Short seed longevity, variable germination conditions, and infrequent establishment events provide a narrow window for *Yucca brevifolia* (Agavaceae) recruitment[1]

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- *Premise of the Study:* The future of long-lived stand-forming desert plants such as *Yucca brevifolia* (Joshua tree) has come into question in light of climate variation and landscape-scale disturbances such as wildfire. Understanding plant establishment dynamics is important for mitigating the impacts of disturbances and promoting revegetation.
- *Methods:* We placed *Y. brevifolia* seeds in shallow caches and manipulated granivore access, nurse shrub effects, and the season of cache placement to determine conditions for seed germination and seedling establishment.
- *Key Results:* Greatest seedling emergence occurred during spring and summer, when increased soil moisture was accompanied by warm soil temperatures. Late winter–spring emergence for cached seeds was enhanced beneath shrub canopies, but seedling survival declined beneath shrubs as temperatures increased in spring. Germinability of seed remaining in the soil was reduced from 50–68% after 12 mo residence time in soil and declined to <3% after 40 mo. Following dispersal from parent plants, seeds are either removed by granivores or lose germinability, imposing substantial losses of potential germinants.
- *Conclusions:* Specific germination and establishment requirements impose stringent limits on recruitment rates for *Y. brevifolia*. Coupled with infrequent seed availability, the return rates to prefire densities and demographic structure may require decades to centuries, especially in light of potential changes to regional desert climate in combination with the potential for fire recurrence. Demographic patterns are predicted to vary spatially in response to environmental variability that limits recruitment and may already be apparent among extant populations.

Key words: Agavaceae; climate conditions; granivory; Joshua tree; Mojave Desert; nurse plants; seed bank; survival analysis; *Yucca brevifolia*.

Germination, emergence, and establishment are the least understood components of plant demography for many desert perennials yet are paramount to understanding population trends, responses to disturbances, and restoration of degraded environments. Changes in community composition and population structure of long-lived perennials can take decades (Bowers et al., 1995; Cody, 2000; Valone et al., 2002; Webb et al., 2003; Guo, 2004) and can easily be overlooked because of the lack of long-term studies in many deserts (Webb et al., 2009). A minimum frequency and magnitude of recruitment are necessary to keep a population from declining (Wiegand et al., 2004). In addition, seedlings are typically more susceptible to environmental extremes, disease, and predation than well-established plants (Kitajima and Fenner, 2000; Meiners and Handel, 2000). Demographic responses to changing environmental conditions will first be evident in the regeneration frequencies of seedlings, which are highly adapted to specific microclimates (Giménez-Benavides et al., 2007; Jackson et al., 2009).

Many factors influence the persistence of desert perennials from the seed through seedling stages. Seeds in the soil surface are susceptible to desiccation, decomposition, and seed predators (Crist and Friese, 1993; Ireland and Andrew, 1995; Espigares and Lopez-Pintor, 2005). In the Mojave Desert, ants and rodents are important seed predators and dispersers (Soholt, 1973; DeFalco et al., 2010), in particular for the arborescent monocot Joshua tree (*Yucca brevifolia* Englem.; Vander Wall et al., 2006; Waitman et al., 2012). Seeds are redistributed by granivores and preferentially placed by scatter-hoarding desert rodents under shrubs (Swartz et al., 2010), dispersed equally between shrubs and open areas (Vander Wall et al., 2006), pilfered from caches in the open (Daly et al., 1992), and transported between shrub canopy and open spaces for later consumption (Swartz et al., 2010). For favorable seedling establishment, the benefits of secondary seed dispersal must balance the costs of seed consumption (Janzen, 1970; Vander Wall et al., 2006). Additionally, seedlings emerging from seed caches may experience competition for limited resources, resulting in higher mortality (Hollander and Vander Wall, 2004; Heleno et al., 2011). In arid environments, nurse plants can modify the soil moisture, temperature, and humidity and protect seedlings against wind and radiation fluxes compared with open locations (Holmgren et al., 1997; Brittingham and Walker, 2000; Legras et al., 2010). By contrast, seedlings beneath shrub canopies may compete for soil moisture when resources are limited (Ogle and Reynolds, 2004).

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An exacting combination of temperature and precipitation may generally be required for desert shrub seedlings to advance to the next life stage (Meyer and Pendleton, 2005). However, large germination events that lead to successful establishment may occur as infrequently as several times per century (Wallace and Romney, 1972). Germination and emergence of desert perennials are associated with infrequent pulse events such as those associated with El Niño–Southern Oscillation (ENSO; Bowers, 1997). In recent decades, these pulse events have also been associated with increases in the frequency and size of wildfires fueled by invasive annual grasses that threaten established populations of *Y. brevifolia* (Loik and Rodgers, 2000; DeFalco et al., 2010). Natural recovery of burned areas is challenged by multiple factors, including loss of seed source plants, alteration of suitable sites for establishment, and limited ranges of scatter-hoarding rodents (Vander Wall et al., 2006; DeFalco et al., 2010; Waitman et al., 2012). Trends of atmospheric warming are predicted for the southwestern United States (Seager and Vecchi, 2010), which may also shift optimum regeneration conditions for *Y. brevifolia* far from the species' present range (Smith et al., 1983; Dole et al., 2003; Cole et al., 2011); however, studies to support this assertion have yet to be conducted. In addition, established plants that have narrow weather requirements for producing and dispersing seeds may be limited because of the rapidly changing climate predicted for arid western North America, but studies are generally lacking for many desert species.

We conducted a field study to understand how seedling emergence and survival are influenced by biotic and abiotic factors in the long-lived desert perennial *Y. brevifolia*. Joshua trees have indehiscent fruits that persist on the trees for months after they first ripen (Rowlands, 1978). Although many of the seeds are gleaned from the trees by rodents, those that persist may disperse later in the fall, winter, and spring (Waitman et al., 2012). We planted seeds during different seasons to simulate secondary dispersal of individual seeds by granivorous rodents (Waitman et al., 2012). We hypothesized that recruitment in *Y. brevifolia* is influenced by a combination of (1) exacting environmental conditions that are seasonal and uncommon among years, (2) positive nurse-plant effects on emergence that translate into enhanced survival of seedlings, and (3) negative granivore effects that reduce seed availability and resulting seedlings. To determine the role of weather, microhabitat, and granivore effects on seedling emergence and survival, we positioned seeds in simulated rodent caches within and outside shrub canopies, as well as inside and outside of protective cages. Final fates of seeds that did not emerge as seedlings were also determined by extracting seeds from the soil and germinating them in the laboratory.

MATERIALS AND METHODS

***Study site*—**Experiments were conducted in Piute Valley, 5 km west of Searchlight, Clark County, Nevada, USA (35.464541°N, −114.95649°W, elevation 1055 m). Soils are in the Lanip-Kinwell association, with gravelly sandy loam to 2.5 cm, gravelly loam from >2.5 cm to 38 cm, and clay loam or gravelly sandy clay loam to 100 cm (Natural Resources Conservation Service, 2011). Mean (± SD) annual total precipitation from 1950 to 2011 for Searchlight is 190 ± 100 mm. Annual precipitation is bimodal, peaking in February and August, and the driest months are May and June (National Climate Data Center [NCDC], 2011). *Larrea tridentata* Cov., *Ambrosia dumosa* (A. Gray) Payne, and *Krameria grayi* Rose & Painter are numerically dominant, whereas *Y. brevifolia* is visually dominant because of its greater height.

***Environmental measurements*—**Precipitation, temperature, and soil moisture were measured at 15-min intervals, starting on 30 December 2008 and continuing through 22 November 2010, using an automated weather-station data logger and temperature and soil-moisture sensors (Hobo, Onset Computer Corp., Pocasset, Massachusetts, USA). Precipitation was measured using a tipping bucket. Temperature was measured at 1 cm below the soil surface. Soil moisture was measured at 5 cm and 25 cm in the open, >1 m from the nearest shrub, using soil-moisture probes.

Seeds and planting design*—Yucca brevifolia* seeds were collected from Piute Valley in July 2007 and visually inspected so that only ripe, intact seeds were selected (i.e., black seeds are known to be viable; B. Waitman, personal communication). Germination was tested before each planting by placing 20 randomly selected seeds on filter paper moistened with deionized water in the dark at room temperature for ≤8 d. Seed germination in all three pretrials, once per planting season, was ≥95%.

A total of 64 plots (46 caged and 18 uncaged) were equally divided between two microhabitats during three seasons in 2009: 12 plots in early winter (January), 12 plots in midsummer (July), and 40 plots in midfall (October and November) of 2009. The microhabitats were either open areas >1 m from the outer canopy of any shrub or within the canopy of *L. tridentata* on the shaded north side of each shrub (nurse plant). In the midfall, 18 of the plots were uncaged for comparison with caged plots to examine the effects of granivory on *Y. brevifolia* seeds and, potentially, the effect of herbivory after seeds germinated. Cages (6-mm wire mesh to exclude rodents) were 50 × 50 × 30 cm and were installed with 15 cm buried below ground (Fig. 1). During each planting, 30 or 36 single seed caches were planted in each plot at 2–3 cm depth and spaced approximately 6 cm apart.

To evaluate seedling survival and seed longevity beyond the duration that we monitored our plots, we included additional plots established at this site from a previous investigation (Waitman, 2009), the fates of which have not been described previously. Those seeds were planted in 80 caged plots in August 2007, equally divided between open and shade microhabitats, in 36 caches; each cache had 2 seeds and was buried 0.1, 2, 3, 4, or 5 cm deep. For both sets of seed experiments, we assumed that all seedlings that emerged had an equal chance of surviving, regardless of age or depth of planting.

***Seedling emergence, growth, and survival*—**New seedlings, including those from the experiments by Waitman (2009), were evaluated monthly during December 2008 through December 2010. When tens to hundreds of seedlings were discovered during a single month's census, they were considered an emergent cohort of that month and/or season. Upon emergence, each seedling was individually marked and mapped. The number of leaves and the leaf color were recorded monthly for each seedling. Purple coloration was assumed to denote drought stress, and if a part of a leaf was yellow, that portion was noted as dead. Seedlings were considered dead if all leaves were completely yellow.

***Seed germinability*—**Seeds that did not emerge during the study were recovered from all plots in fall 2010 by excavating and sifting the soil on entire plots. Recovered seeds that were completely intact and without holes, cracking, or flaking were tested for germinability and compared with pretrial/storage germinability. Stored and recovered seeds represented five levels of soil residence time: 0 mo (never planted, stored), 12–13 mo (planted October–November 2009), 17 mo (planted July 2009), 23 mo (planted January 2009), and 40 mo (10 plots from August 2007). We expected caged and uncaged seeds to experience similar conditions with respect to effect on germinability, so only caged seeds were used. Seeds were distributed in sterile Petri dishes lined with filter paper at an approximate density of 7 seeds per plate. Filter papers were wetted with deionized water, and dishes were covered to maintain high humidity. Petri dishes were placed randomly in a dark environment at 25°C and were checked daily for 8 d for the emergence of radicles. Seeds were turned once per day to minimize the growth of mold.

***Statistical analyses*—**All analyses were conducted using R statistical software version 2.12 (R Development Core Team, 2008). Analysis of variance (ANOVA) was used to test for differences in emergence between treatments by first transforming data using arcsine-square root, and equal variance was assessed using Levene's test. A three-way ANOVA was performed with the proportion of seed emerging as the dependent variable and with planting season (PS), microhabitat (Micro), and emergence cohort (Cohort) as the independent variables. Emergence data were split into two factor combinations.

Fig. 1. Joshua tree (*Yucca brevifolia*) stand at Joshua Tree National Park, Riverside County, California. Left inset illustrates the cages designed to exclude rodents to monitor Joshua tree germination and establishment. Right inset illustrates the size of a representative 2-yr-old Joshua tree seedling with a 1-cm grid as a backdrop.

The first combination included two planting seasons (January and July 2009) and the three emergence cohorts (September 2009, January 2010, and April 2010). The second ANOVA included all the planting seasons (i.e., October and November 2009 as well as the first two) and only used the January and April 2010 emergence cohorts (because seedlings emerging in September 2009 could not have resulted from seeds planted after that in October and November 2009).

An ANOVA was performed on the proportion of seed recovered from the total planted per plot using cage (Caged) and microsite (Micro) as factors. No transformation was necessary after data were assessed using Levene's test. A 2×5 contingency table was used to test for differences in the proportion of germinable seeds between caged and uncaged plots and among residence times in the soil. Germination in the two microhabitats were analyzed separately.

We used the Cox proportional hazard model in the "Survival" package in R to test for differences in seedling survival because it is more robust to issues of distribution than the log-rank test (Fox, 2002; Bewick et al., 2004). We reviewed the Wald test, score test, and the likelihood ratio test; because the results were very similar, we report the latter results. Kaplan-Meier estimates were used to graphically illustrate differences in survival among treatments. For each emergence cohort, we compared survival by seed cache sizes (one or two seeds) or microhabitats (open or shade). Because emergence data were collected in an incomplete design, we analyzed emergence data in separate two-factor combinations.

RESULTS

***Abiotic conditions associated with emergence events*—**New seedlings emerged as a group and were collectively considered an emergent cohort for each season. Seedlings emerged within three cohorts throughout the study: September 2009, January 2010, and April 2010. The largest associated precipitation events and the resulting days of shallow soil moisture $\geq 0.10\ m^3 \cdot m^{-3}$ during the period of emergence occurred during 19–22 January 2010 (64 mm, 12 d) and the prior summer (22–23 August 2009; 41 mm, 5 d (Fig. 2). Another event during 6–9 March 2010 (29 mm) was preceded by shallow soil moisture $>0.10\ m^3 \cdot m^{-3}$ due to smaller storms since mid-January, and this March event prolonged soil moisture for an additional 13 d. Daily soil temperature ranges for the days of high soil moisture following these three storms were 20.9–34.8°C (August 2009), 2.7–8.9°C (January 2010), and 6.2–18.2°C (March 2010), respectively. Smaller storms resulted in fewer days of elevated surface soil moisture: 2–3 July (32 mm, 4 d) and 20 July 2009 (15 mm, 3 d); 7 December 2009 (21 mm, 2 d) and 7–9 February 2010 (24 mm, 5 d). Soil for this study area was saturated at approximately

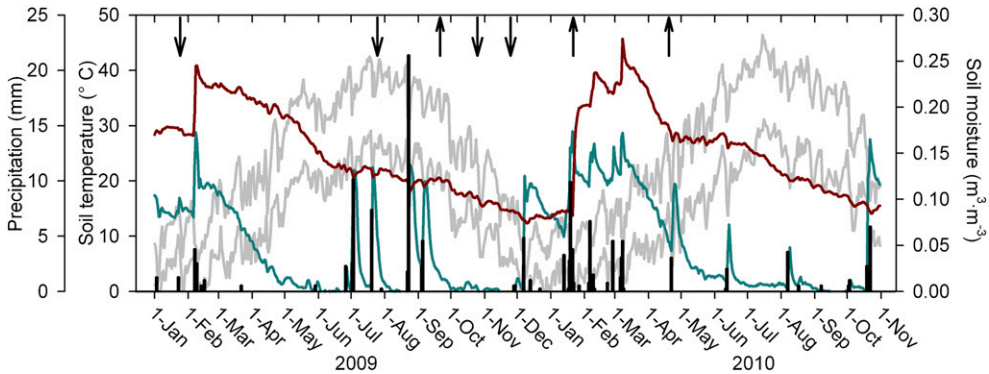

Fig. 2. Daily environmental conditions during the study of emergence and survival of *Yucca brevifolia* seedlings, including precipitation (black bars), minimum and maximum soil temperature at 1 cm depth (lower and upper gray lines, respectively), as well as shallow (5 cm, blue line) and deep soil moisture (25 cm, red line). Downward-pointing arrows denote when seeds were planted; upward arrows denote when seedling cohorts emerged.

0.36 $m^3 \cdot m^{-3}$. Surface soil moisture reached highs with daily ranges between 0.19 and 0.21 $m^3 \cdot m^{-3}$ after precipitation pulses, whereas prolonged dry periods in hot months (May–November) lowered daily surface soil moisture to ≤0.018 $m^3 \cdot m^{-3}$. Deep soil moisture was highest following the February 2009 and late-January through March 2010 precipitation events (0.25 and 0.28 $m^3 \cdot m^{-3}$, respectively); considerable soil drying at this depth began in mid-May 2009 and April 2010 and continued through the summer and fall to reach a minimum before cool-season precipitation (0.08 $m^3 \cdot m^{-3}$; Fig. 2). Total precipitation by month peaked in February and July 2009 and in January 2010 (52, 64, and 78 mm, respectively), whereas no precipitation occurred in April and October 2009 or in May and July 2010. In 68% of years on record, at least 1 mo between July and October received >45 mm of precipitation (NCDC, 2011).

Seedling characteristics—Most 1-mo-old seedlings were found with a single cotyledon (73%) and occasionally one (27%) or two (<1%) primary leaves and were ≤6.9 cm tall (mean ± SD = 3.5 ± 1.28 cm, n = 593). One-year-old seedlings grew to ≤7.7 cm tall (4.0 ± 2.0 cm, n = 51), with one (35%), two (49%), three (12%), or four (4%) leaves. Finally, 2-yr-old seedlings grew to ≤10.2 cm tall (mean = 6.4 ± 2.7 cm, n = 14) and had ≤4 leaves, with some senescence of the cotyledon and earlier leaves apparent (Fig. 1). At 2 yr, mean basal stem diameter was 3.3 ± 2.0 mm (n = 14, minimum = 1.3 cm, maximum = 5.7 cm). We also observed seedlings that we deemed to be deceased because all of the stems were completely brown. Subsequently those individuals produced new green leaf material, which indicated that caution should be used in determining status.

Seedling emergence for different planting seasons—Caged and uncaged plots from the October and November 2009 planting season had marginally different proportions of seedling emergence (0.23 vs. 0.11, respectively) when averaged over January and April 2010 emergence cohorts (t = 1.8, df = 14.6, P = 0.09). The uncaged plots were excluded from further emergence comparisons to remove the effects of mammalian granivory. By April 2010, the proportion of seeds of the original 36 plants/plot that did not emerge were approximately 0.74, 0.94, 0.75, and 0.82 in the January, July, October, and November planting groups, respectively. Across all available planting seasons, the greatest proportion of seedlings emerged for the cohorts during the warm months of September 2009 (0.14) and April 2010 (0.11) compared with the cohort that emerged during the cooler month of January 2010 (0.01). The proportion of *Y. brevifolia* seedlings that emerged (averaged over planting seasons) was 1.43× higher in the shade than in the open (Micro, $F_{1,60}$ = 7.9, P < 0.01). The proportion of seedlings emerging in September 2009 was approximately 6× greater for the seeds planted the prior January compared with those planted the prior July, but emergence in January and April 2010 was similar between these planting seasons (Fig. 3A; PS × Cohort, $F_{2,60}$ = 22.0, P < 0.01); no other two- or three-way interactions among Micro, PS, and Cohort were significant at P < 0.05. When all planting seasons were analyzed together, the proportions of seedlings that emerged in January 2010 were similar, but emergence 3 mo later in April were higher for the seeds planted the prior October and November 2009, compared with the other planting seasons (Fig. 3B; PS × Cohort, $F_{3,76}$ = 36.4, P < 0.01). Neither microhabitat nor other interactions were significant.

Seedling survival—Among the 128 seedlings that emerged in September 2008 (Waitman, 2009), 82% died within the first 12 mo (September 2008 to September 2009), whereas only

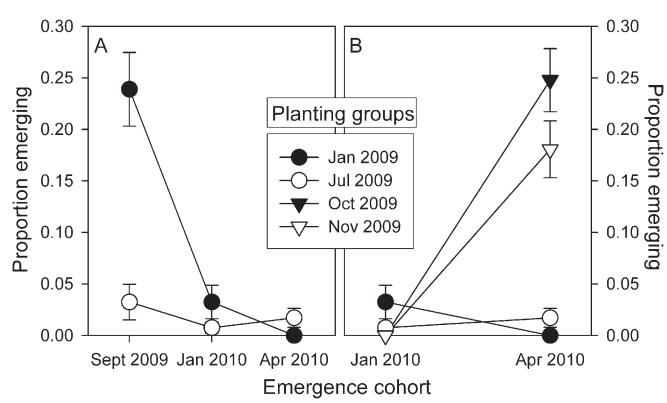

Fig. 3. Mean proportion (± SE) of *Yucca brevifolia* seedling emergence from seeds planted during 4 mo in 2009. Proportion of seedlings that emerged was based on the seeds still present after prior emergence was removed. (A) Seedlings that emerged during 3 mo (September 2009, January and April 2010) from seeds planted in January and July 2009. (B) Seedlings that emerged during January and April 2010 from seeds planted in all 4 mo in 2009.

0.08% of the original cohort (4% of those remaining) died in the subsequent 8 mo. Most mortality occurred during April through June 2009. By July 2009, mortality tapered off, and at the conclusion of the study in December 2010, 7 seedlings (5%) remained, reaching an age of 28 mo. For the plots that we established close to those of Waitman (2009), 469 seedlings emerged in the three cohorts during January 2009 through December 2010. The percentage of seedlings alive 3 mo after emerging was lowest for those that emerged in January 2010 (64%) and highest for those that emerged in September 2009 (94%). Those that emerged in January or April 2010 did not survive for 12 mo, whereas 6 (3%) of that emerged in September 2009 survived to the conclusion of the study, or 16 mo.

Seed caches—For seedlings that emerged in September 2008 or September 2009, seedling survival was not different between multiple seed caches and single caches ($\chi^2 = 1.3$, df = 1, $P = 0.26$ and $\chi^2 = 2.5$, df = 1, $P = 0.11$, respectively). Only single seedlings emerged from two-seeded caches in January and April 2010, precluding the comparison of multiple and single seed caches for the remainder of the analyses.

Microhabitat—Microclimate did not affect survival in the September 2008, September 2009, and January 2010 emergence cohorts ($\chi^2 = 0.6$, df = 1, $P = 0.44$; $\chi^2 = 0.3$, df = 1, $P = 0.60$; and $\chi^2 = 2.5$, df = 1, $P = 0.11$, respectively). Although it appears that seedling survival under *L. tridentata* was greater than that in open areas (Fig. 4), sample size provided insufficient power to detect differences. Only for seedlings that emerged in April 2010 was there a significantly lower survival for those beneath *L. tridentata* canopies ($\chi^2 = 6.1$, df = 1, $P = 0.01$).

Fate of seeds remaining in soil—Seeds were recovered and classified into two groups: those that germinated or degraded in the soil and those that were intact and tested in the laboratory for germinability. We successfully recovered seeds from caged plots, with 78% recovered after 12 mo and 81% after 40 mo in the surface caches. The remainder that were not accounted for likely decomposed underground and were not recovered. By contrast, only 26% of seeds were recovered from the uncaged plots after 12 mo. Assuming that 22% of those seeds also decomposed, 52% of unaccounted seeds are estimated to be removed by mammalian granivores. Also, significantly more intact seeds were recovered from caged plots (mean ± SD = 9.1 ± 4.3 seeds, or 25%) than from uncaged ones (2.6 ± 3.8 seeds, or 7%) (Caged, $F_{1,30} = 18.8$, $P < 0.01$); there was no difference between open and shaded microsites and no interaction.

After incubating recovered seeds on Petri plates, emergence of radicles peaked at 2 d (46% of seeds) and most seeds germinated after 4 d (93%). Examining only caged plots, the proportion that germinated from the total planted, adjusting for those that had germinated throughout the study, was reduced with increasing residence time in the soil in both shade ($\chi^2 = 447.9$, df = 4, $P < 0.01$) and in the open ($\chi^2 = 510.6$, df = 4, $P < 0.01$). Twelve months in the soil reduced germination to 50–68%, and it dropped to less than 1–3% after 40 mo in the soil (Table 1).

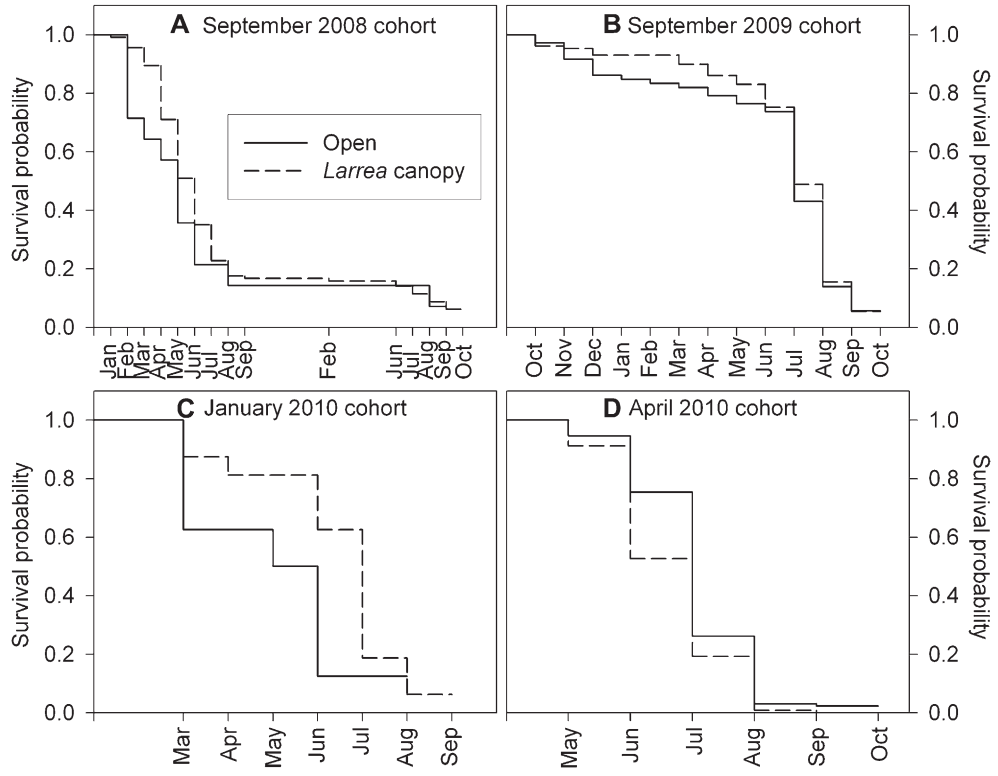

Fig. 4. Kaplan-Meier functions illustrating differences in *Yucca brevifolia* seedling survival between *Larrea* canopy and open microhabitats for seedlings that emerged in (A) September 2008, (B) September 2009, (C) January 2010, and (D) April 2010. See text for statistical explanation of survival between canopy and open microhabitats.

TABLE 1. Germination of *Yucca brevifolia* seeds recovered from simulated seed caches residing in the surface soil for various durations. Control represents stored seeds that were never planted at the Searchlight, Nevada, study area.

	Germination (%)		
Duration (mo)	*Larrea* canopy	Open	Control
0	na	na	97.3
12	67.5	50.0	na
17	6.3	23.3	na
23	6.5	20.7	na
40	3.2	2.5	na

DISCUSSION

Granivore pressure and rapidly diminishing seed germinability collectively limited the abundance of *Y. brevifolia* seeds available for establishment. Small mammals reduced the number of simulated subsurface caches in uncaged plots compared with caged plots. Upon locating caches, mammals likely either consumed seeds or recached them (Vander Wall et al., 2006), thus eliminating those seeds from further observation. Similarly, seeds of *Y. brevifolia* that fell to the soil surface were rapidly removed by seed predators/facilitators in days to weeks in other studies (Waitman, 2009), as observed for other seed predators of perennial plants (Roth and Vander Wall, 2005; Beck and Vander Wall, 2010). Seeds that were not lost to granivores rapidly lost germinability through time. Longevity of seeds in the soil declined by about 50% per year, which indicates that *Y. brevifolia* has little capacity for seed dormancy. This lack of longevity in the seed bank is consistent with the long-lived shrub *Coleogyne ramosissima*, which frequently co-occurs with *Y. brevifolia* in the Mojave Desert and does not produce persistent seed banks (Meyer and Pendleton, 2005).

The emergence of multiple seedling cohorts among seasons during this brief study indicates that *Y. brevifolia* has frequent opportunities for germination, although the magnitude of emergence was variable. As hypothesized, overall emergence in our study was enhanced beneath the nurse plant *L. tridentata* compared with the shrub interspaces (Brittingham and Walker, 2000). In addition, the greatest seedling emergence occurred when rainfall events coincided with warm temperatures in September and April. Soil moisture in the top 5 cm of soil, where seeds are typically cached (Vander Wall et al., 2006; Waitman et al., 2012), remained high (>0.10 $m^3 \cdot m^{-3}$) for up to 2 wk following >29 mm of precipitation. We know from a controlled temperature experiment using the same seed source that emergence under moist soil conditions occurs within 7 d (L. A. DeFalco, unpublished data). Furthermore, the experimental night:day temperatures of 15°C:25°C and 20°C:30°C were optimal for *Y. brevifolia* seedling survival (mean ± SD; 54.5 ± 22.3% and 73.9 ± 11.5%, respectively), but survival declined below a temperature range of 10–20°C (12.5 ± 14.6%). This pattern is consistent with the large emergence in September and April and the low emergence in January. Interestingly, the low emergence of seeds planted 2 mo prior to the September 2009 rainfall event (that resulted in high emergence of seeds planted several months before) suggests that factors other than warm, wet conditions may be important for optimal emergence.

We also observed a low rate of emergence in January, when surface soil moisture was comparable to September and April events but temperatures were colder. January emergence indicates plasticity in the ability of this species to emerge across seasons, which may be generally rare in Mojave Desert perennial species (Ackerman, 1979; Baskin and Baskin, 1998). After reviewing 24 climate models, Seager and Vecchi (2010) predicted that the southwestern United States will become drier and warmer overall, but that a shift in winter precipitation from snow to rain will result in wetter winters (Mote et al., 2005, Knowles et al., 2006). Flexibility of emergence timing could benefit *Y. brevifolia* populations, especially west of −117° longitude (e.g., west of Barstow, San Bernardino County, California), a region that currently experiences a winter-dominated cool precipitation pattern (Hereford et al., 2006). In future climate scenarios, the ability for flexible timing of *Y. brevifolia* emergence could provide the potential for adaptation to shifting climate conditions.

High germinability within the first year and broad emergence of *Y. brevifolia* during periods of increased soil moisture and warm weather indicate adaptation to regular summer rainfall. In general, seeds mature and disperse from the parent plant immediately before summer monsoonal storms; at our site, about 24% of precipitation falls in July and August (NCDC, 2011), which would result in germination of seeds in late summer. In our study, large numbers of *Y. brevifolia* seedlings emerged after >29 mm of rain fell in a single month, and soil moisture remained high for several days. When compared to the climate record for our site, favorable precipitation conditions for seedling emergence occurred in about 68% of summers, which suggests that conditions conducive to emergence events might be more common than expected on the basis of our low detection of *Y. brevifolia* seedlings in the field (M. B. J. Reynolds et al., personal observation). However, summer precipitation decreases on a southeast to northwest gradient across the entire range of *Y. brevifolia* and, thus, conditions conducive to emergence are expected to decline in frequency across that gradient in relation to less summer precipitation. This pattern implies that there are fewer opportunities of emergence in the far western Mojave Desert, and under the current climate regime *Y. brevifolia* in that area may be most vulnerable to demographic change resulting from low and infrequent recruitment and may already have occurred.

Despite a high frequency of favorable emergence conditions, illustrated by the historical climate at our site, infrequent conditions for seedling establishment may dampen positive demographic responses in this species. *Yucca brevifolia* had greatest survival for seedlings that emerged in late summer, when summer rainfall had commenced, and after months of extended warm temperatures and the period of summer soil-moisture deficit had passed. As with perennials in Mediterranean ecosystems, most *Y. brevifolia* seedling deaths occurred in the first dry period after emergence and before summer rains (Lloret et al., 1999); for the Mojave Desert, this vulnerable period typically starts in May and June. Although seedling emergence in April was comparably higher than that in September, the relatively short growing period following emergence may put the seedlings at a developmental and competitive disadvantage because they have insufficient time to develop roots in the deeper soil profile where soil moisture is more reliable and soil temperature less extreme. We expect that September-emergent seedlings developed deeper roots throughout the fall and winter. Those plants enter the dry months of the following spring and summer more well developed, allowing access to deeper soils and greater growth even as soil moisture is depleted and temperatures decrease

(Leishman and Westoby, 1994), or they simply survive maintenance needs during dormancy. For other long-lived perennials, pulses of rainfall associated with ENSO have provided conditions conducive to appreciable recruitment (Bowers, 1997; Holmgren et al., 2006). After germination, a strong ENSO bringing abundant winter and early spring precipitation is likely to provide the conditions most conducive to establishment of *Y. brevifolia*.

Nurse plants in arid environments are known to moderate insolation, soil moisture, temperature, and humidity beneath their canopies and improve conditions for seedling establishment (Lowe and Hinds, 1971; Holmgren et al., 1997; Drezner, 2006). Furthermore, seeds are redistributed by granivores and preferentially placed under shrubs by scatter-hoarding desert rodents (Swartz et al., 2010), dispersed equally between shrubs and open areas (Vander Wall et al., 2006), pilfered from caches in the open (Daly et al., 1992), and transported between shrub canopy and open sites (Swartz et al., 2010). The overall emergence of *Y. brevifolia* in our study was enhanced beneath the nurse plant *L. tridentata* compared with the open spaces between shrubs. Brittingham and Walker (2000) also found that *Y. brevifolia* plants established beneath nurse-plant canopies more often than by random chance. After emergence, nurse plants in our study had no effect on the establishment of summer-emergent cohorts. All the seedlings protected by cages were included in our survival analysis; they were not exposed to herbivory, which could have significant effects on survival of small Joshua trees (DeFalco et al., 2010). At least for seedlings that emerged in April, lower survival beneath *L. tridentata* canopies compared with open spaces implies a shift from facilitation of seedlings by adult shrubs to competition between seedlings and their nurse plants. Gradual depletion of deep soil moisture beneath *L. tridentata* through the growing season may amplify competition with *Y. brevifolia* seedlings (Brisson and Reynolds, 1994), particularly for these April-emergent seedlings that had less time to develop roots and shoots than the September-emergent seedlings.

In summary, the dynamics of germination, emergence, and seedling survival in *Y. brevifolia* are fundamental to understanding current and future threats to populations of this iconic desert species. Natural regeneration of other desert perennials overlaps with infrequent periods of heavy precipitation correlated with ENSO (Bowers, 1997; Holmgren et al., 2006). Paradoxically, precipitation pulses that stimulate large seedling-emergence events also produce abundant production of invasive annual grasses, which fuel large-scale desert wildfires and put *Y. brevifolia* at risk (Loik and Rodgers, 2000, DeFalco et al., 2010). Re-establishment of *Y. brevifolia* in burned areas may first require initial establishment of nurse plants in combination with facilitation by animal dispersal agents (Loik and Rodgers, 2000; Vander Wall et al., 2006) and very specific environmental conditions suitable for establishment. The return of *Y. brevifolia* to prefire densities and demographic structure may take decades to centuries or be entirely unlikely (Carpenter et al., 1986; Comanor and Clarke, 2000; Webb et al., 2003; Guo, 2004), especially in light of potential changes to regional desert climate in combination with plant invasions and the potential for recurrence of subsequent fires. Even in the absence of the invasive species-driven fire regime, the ability of *Y. brevifolia* to contend with climate changes, as suitable establishment conditions vary through space and time, may be challenged (Cole et al., 2011). Future efforts to quantify other *Y. brevifolia* life stages are important for accurate predictions of the future prospects for *Y. brevifolia* and the unique plant communities that they represent.

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