RESEARCH ARTICLE

Seedling Ecology and Restoration of Blackbrush (*Coleogyne ramosissima*) in the Mojave Desert, United States

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Abstract

Increases in fire frequency are disrupting many ecological communities not historically subjected to fire. In the southwestern United States, the blackbrush (*Coleogyne ramosissima*) community is among the most threatened, often replaced by invasive annual grasses after fire. This long-lived shrub is vulnerable because it recruits sporadically, partially due to mast seeding and the absence of a seed bank. The goal of this study was to evaluate if shrub restoration can be enhanced by identifying and ameliorating recruitment limitations. Specifically, we tested the effect of encapsulating seeds in predation-deterring "seed balls." We also tested the effects of nurse plants and mammalian exclusion cages on seedling emergence, growth, and survivorship. These experiments were conducted in a full-factorial design across three sites differing in elevation. Over 2 years, 13% of all planted seeds emerged and the effect of seed balls was overwhelmingly negative because of low emergence.

Nurse plants had overall positive effects at Low Elevation, but negative effects at Mid- and High Elevation. Emergence and survival were highest in caged plots everywhere, and effect sizes increased with elevation. Interactions between the cage and the nurse plant treatments indicated that nurse plants tended to attract mammalian predators, lowering emergence and seedling survivorship, particularly at higher elevations. Findings conform to the stress-gradient hypothesis in that interactions among seedlings and mature plants shifted from facilitation to competition as environmental stress decreased with increasing elevation, suggesting that they are transferable to ecologically similar communities elsewhere. Knowledge of site-specific recruitment limitations can help minimize ineffective restoration efforts.

Key words: climate change, disturbance, elevation gradient, nurse plants, rodents, seed balls, seed bank, stress gradient, survivorship.

Introduction

Communities vary in their abilities to tolerate disturbance. Those that evolved under high disturbance frequencies, e.g. grasslands, chaparrals, and rocky intertidal shores, tend to be resilient to historical and novel causes of disturbance (Sousa 1984). Communities that evolved under low disturbance, e.g. boreal forests, arid shrublands, and coral reefs, are generally more vulnerable, e.g. to fire (Condon et al. 2011), insect outbreaks (U.S. Forest Service 2010), or high temperature (Diaz-Pulido et al. 2012). Full recovery of these communities after large-scale destruction is uncertain because the dominant species often recruit infrequently, grow slowly, and are therefore regularly replaced by pioneering invasive species (Hobbs & Huenneke 1992).

In these vulnerable communities, the restoration challenge is to accelerate recruitment, e.g. by broadcasting propagules in high numbers (Nelson et al. 1970). But this approach often remains ineffective because of low survivorship (Abella 2009). Here, we evaluated methods for improving emergence and early seedling survivorship by testing which environmental and biotic factors most constrain recruitment. Particularly, we examined if positive nurse plant effects and negative predation effects varied with elevation.

The study was conducted in the blackbrush (*Coleogyne ramosissima*) community of the southwestern United States, which occurs primarily in the Mojave and Great Basin Deserts between 750 and 1,900 m elevation (Meyer & Pendleton 2005). In its core zone, blackbrush forms near-monocultures that benefit many animal species, while also protecting the soil (Shreve 1942). Recent increases in frequent and severe wildfires have reduced the extent of this community (Brooks & Matchett 2006). Recovery is slow even in the best circumstances, but today it is additionally impeded by invasive exotic annual grasses (e.g. *Bromus rubens*; Abella 2009) that promote a frequent fire cycle (Brooks & Matchett 2006). As blackbrush does not resprout and rarely recruits, it may take centuries to millennia for blackbrush to reestablish after fire (Lovich & Bainbridge 1999).

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In most years, recruitment is essentially zero because nearly all seeds are consumed by rodents, and those that escape predation frequently die from desiccation (Lovich & Bainbridge 1999). Recruitment follows mast seeding only if the following spring is exceptionally wet (Meyer & Pendleton 2005). There are multiple restoration techniques to increase establishment rates, e.g. by broadcasting seeds inside seed balls, using predator exclusion cages, or seeding under nurse plants.

The seed ball method (Fukuoka 1978) has been used in agriculture and grassland systems, but has not been tested in arid regions with woody species. Seed balls made from clay, fiber, and humus are thought to eliminate seed predation, promote germination by retaining moisture, and facilitate growth through nutrient enrichment. In the absence of rain, eliminating seed predation may also increase persistence of a short-term seed bank until better conditions arise.

The benefits of predator exclusion cages depend on predation pressure, which varies over time and space (Stapp & Polis 2003). In the Mojave Desert, rodent abundance increases with elevation along a productivity gradient (Price et al. 2000). Given the high cost of exclusion cages, it is important to know where they would be most effective.

Adult shrubs may provide a more benign microenvironment for establishment compared to bare interspaces (Niering et al. 1963), and this has been exploited in restoration by placing seeds or transplants near such "nurse plants." However, nurse plant effects are complex in that they are expected to be net-positive only in harsh environments, shifting to net-negative as stress decreases and resource competition increases (Bertness & Callaway 1994). Negative nurse plant effects can also be consumer-mediated (Chaneton et al. 2010), and more likely to occur between more closely related species (Verdu et al. 2012). Moreover, nurse plants can facilitate the establishment and performance of invasive species (Abella & Smith 2013).

We investigated the restoration techniques of seed balls, mammalian exclusion cages, and nurse plants at three elevations to examine which technique, alone or in combination, resulted in the highest seedling emergence rate, growth, and survivorship for blackbrush in the Mojave Desert. We did not replicate elevation, however, the slope with our three sites was representative of an extremely common landscape pattern in this desert, where at low elevation a *Larrea tridentata*/*Ambrosia dumosa* community grades into a transition community dominated by *Yucca brevifolia*, and then into blackbrush monoculture at higher elevation (Beatley 1975).

We hypothesized that seed balls would benefit emergence the most at intermediate elevation within the blackbrush range because at lower elevation seed balls may inhibit emergence due to greater aridity, whereas at higher elevation water may not be the primary constraint. Further, we hypothesized that the positive effects of cages on emergence and survivorship would increase with elevation due to increasing rodent densities. Finally, we hypothesized that the positive effect of nurse plants would be stronger at lower elevation, where heat exposure is higher, and under heterospecific nurse plants that signal to predators a different type of food than the seeds of the target species.

Methods

Site Description

The study site is located on U.S. Bureau of Land Management property near the Mojave National Preserve in southern California. Mean annual temperature is 14.4°C with an average summer high of 33.8 °C and winter low of −1.4°C. Mean annual precipitation is 212 mm (52 years on record; WRCC 2008). Three experimental sites were selected to cover the density range of the blackbrush community in this region. At the Low Elevation Site (1,260 m; 35°28′25.87″N, 115°38′12.95″W), creosotebush (*Larrea tridentata*) is the dominant species whereas blackbrush is uncommon. The Mid-Elevation Site (1,305 m; 35°28′41.41″N, 115°37′42.58″W) is situated within a transition zone with about equal cover of creosotebush and blackbrush. The High Elevation Site (1,510 m; 35°28′25.76″N, 115°35′31.89″W) is typical of a blackbrush-dominated community. Soils conformed to typical variation in elevation for this region such that soils were sandier at higher elevation, and more loamy at lower elevation, with all sites having a high gravel content (Beatley 1975).

To capture climatic differences, we installed a rain gauge (EcH$_2$O Rain model ECRN-50, Decagon Devices, Inc., Pullman, WA, U.S.A.) at each site and four soil moisture and temperature probes (EcH$_2$O EC-TM, Decagon Devices, Inc.) at 10 and 30 cm soil depth (two at each depth). Sensor readings were logged in 15-minute intervals (Em50 EcH$_2$O logger, Decagon Devices, Inc.).

Experiment I Design

At each site, we implemented a balanced, fully factorial three-factor experimental design with each treatment combination replicated three times. The factors were seed ball (with/without), cage (with/without), and nurse plant (near shrub/in the open). In error, there was one additional caged plot and a missing uncaged plot at the High Elevation Site and the statistical analysis was adjusted accordingly. The dominant shrub species at each site served as nurse plants: creosotebush at Low Elevation, blackbrush at High Elevation, and both at Mid-Elevation.

Comstock Seed supplied the seeds (Gardnerville, NV, U.S.A.), reporting 97% viability. In the months before seed application, seeds were cold-stored, meeting conditions for cold-stratification that improves germination rates (Dreesen & Harrington 1997). Germination rates for blackbrush are usually high, between 40 and 90% (Dreesen & Harrington 1997).

The experimental unit was a 70 × 70−cm plot, placed haphazardly, that received 150 blackbrush seeds. Seeds were applied in a regular grid pattern with three seeds per grid point, either buried directly 3−5 mm deep or inside seed balls that were half-buried. The seed balls were made of 28 volume units organic garden soil, 11 units dry red clay, 11 units coconut fiber, and 5 units sand and they were air-dried for storage and transport. Finished balls were approximately spherical with 40 mm diameter. Herbivore exclusion cages, made from galvanized steel hardware cloth (1.25-cm mesh), were installed

immediately after seeding. They were buried 15 cm deep and extended 15 cm above the soil surface. Near-nurse plant plots were positioned on the north side of mature shrubs, close to the main stem, whereas open plots were positioned at least 1 m away from the nearest shrub.

Experiment II Design

Because of extremely low emergence from seed balls in Experiment I, we conducted a second, short-term experiment to test two new seed ball recipes with less clay. We also made the balls smaller and flatter (diameter = 30 cm, thickness = 20 mm) to increase the surface area:volume ratio. The experiment was conducted at the same sites, with the same number of seeds per plot, but we omitted the cage and nurse plant treatments, placing all plots in the open. The replication number was increased to 4. Thus, with two types of seed balls and the bare seed control, the total plot number per site was 12.

Tracking Emergence and Survivorship

For Experiment I, plots were seeded between 30 January and 1 February 2010, whereas for Experiment II on 23 November 2010. Plots were censused for seedling emergence, presence/absence of seedlings, and leaf number in irregular intervals between March 2010 and May 2012. We tracked individual seedlings using unique markers and a coordinate map system for each plot. We conservatively assumed that seedlings were "alive" when the central stem was still standing, except on the last census of 2012, when we counted only seedlings with green leaves as "alive." No blackbrush emergence was observed outside of the plot areas, thus we excluded that establishment from the natural seed bank influenced the results.

Data Quality Control and Statistical Methods

For Experiments I and II, we analyzed cumulative seedling emergence, whereas for Experiment I, we also analyzed survivorship and leaf number. We assumed the Poisson distribution for cumulative emergence in a generalized linear model (GLM) in SPSS v.19 (IBM Corporation, Armonk, NY, U.S.A.). We constructed Kaplan–Meier survivorship curves for seedlings based on the dates of emergence and disappearance and determined significant treatment effects with a log-rank test. Treatment effects on leaf number were analyzed by repeated measures analysis of variance (ANOVA) in SPSS.

We first analyzed the treatment effects separately for each site, as the experimental design was not exactly repeated at each elevation (nurse plant species changed). We conducted site comparisons on subsets of data for which direct comparisons were possible: (1) plots without nurse plants across all three sites; (2) plots in the open and next to creosotebush at Low and Mid-Elevation; (3) plots in the open and next to blackbrush at Mid- and High Elevation. As sites were not replicated within elevation, the *p* values we report for site

comparisons apply strictly to the specific populations of this experiment. However, it is our view that elevation probably played a large role in generating population differences across sites.

Owing to very low emergence from seed balls in Experiment I, we omitted seed ball plots for the analysis of cage and nurse plant effects.

Results

Precipitation, Soil Moisture, and Temperature

Cumulative precipitation showed little difference across the three elevations until October 2010 (Fig. S1a, Supporting Information). Afterwards, data loss at Mid- and High Elevation from 7 October to 23 November 2010 probably exaggerated the true difference in cumulative precipitation across sites. Thus, increases in soil moisture with elevation (Fig. S1b & S1c) were likely the result of decreases in temperature (Fig. S1d & S1e) and evaporation demand, rather than site differences in precipitation. For the critical period of blackbrush germination and growth (October through April), precipitation was 88% (2009/10), 140% (2010/11) and 28% (2011/12) of the average for this region (Hereford et al. 2004).

Seed Ball Effects

In Experiment I, a total of 1,653 seedlings emerged from the 12,600 seeds planted (13%). The emergence ratio was significantly higher for bare seeds ($p < 0.001$); across all plots, 1,365 seedlings emerged from 6,300 bare seeds (22%), compared to 288 seedlings from 6,300 seeds inside seed balls (5%). Most (50 + %) seed ball emergence happened in the second spring and at Mid- and High Elevation. At Low and Mid-Elevation, seedlings from bare seeds had more leaves than those from seed balls ($p < 0.001$; Fig. 1a–b), though the difference diminished over time.

In Experiment II, 72 seeds emerged from 5,400 seeds planted (1%). There was no significant difference in emergence between the two seed ball recipes and emergence from bare seeds was again higher, except at Mid-Elevation where emergence was not different between treatments ($p < 0.001$, 0.370, 0.002 for Low, Mid- and High Elevation, respectively). The rates of emergence in Experiment II were 17% and 0.44% from bare seed and seed ball respectively, equivalent to an odds ratio of 39:1. Comparing Experiment II with the equivalent treatment group of Experiment I (no cage, no nurse plant), the rates of emergence were 13.7% and 0.15% from bare seed and seed ball, respectively, an odds ratio of 91:1.

Cage and Nurse Plant Effects

Tables 1–3 summarize the effects of cage and nurse plant by site for bare seed plots only. Cages positively influenced growth at High Elevation (Fig. 1f) and they had predominantly positive effects on emergence (Fig. 2) and survivorship (Fig. 3) at all elevations (Tables 1–3). However, nurse plant effects varied
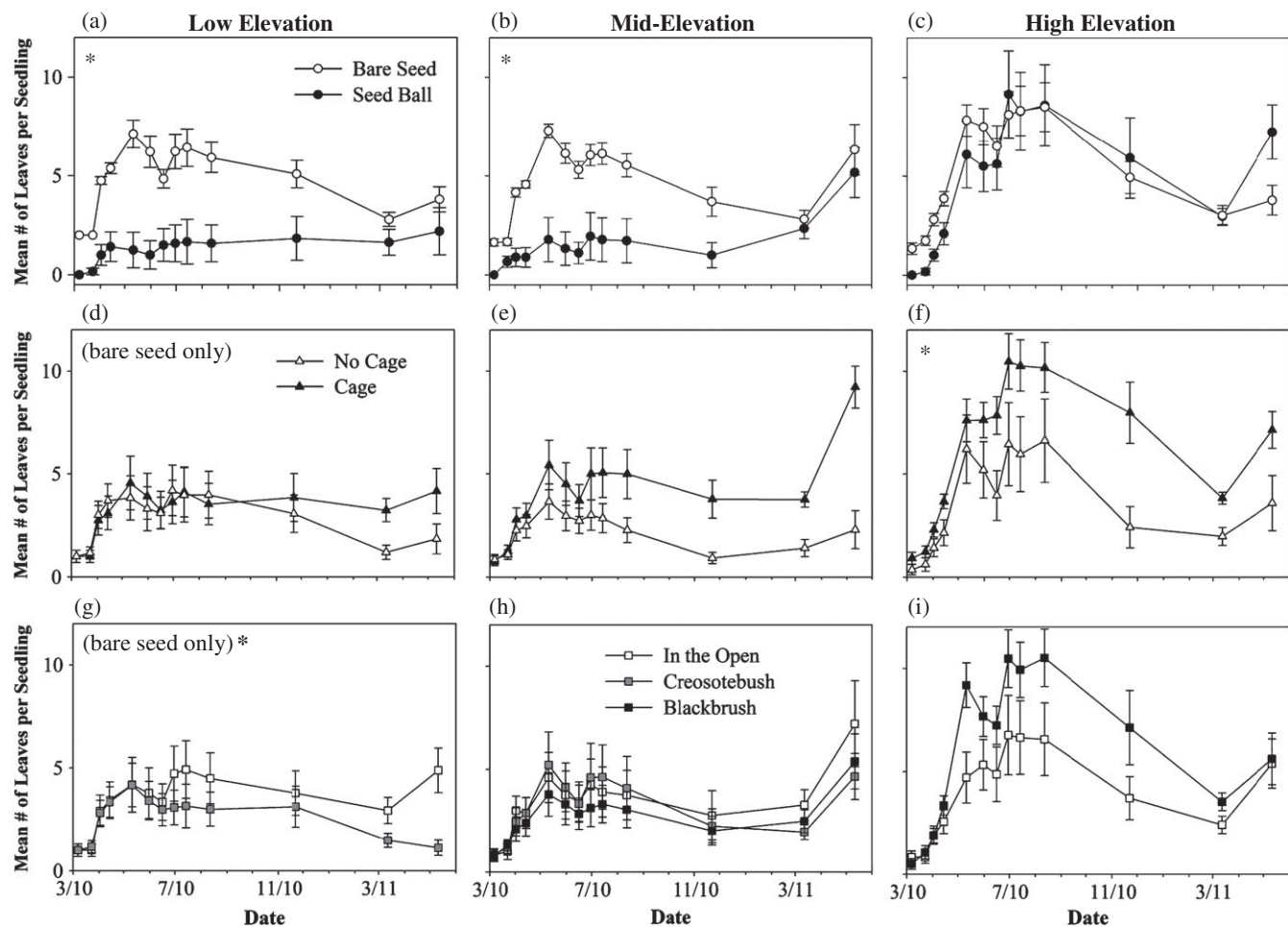
Figure 1. Average number of leaves per seedling with standard error bars of the mean at each site over the course of the study period. The first row (a–c) shows the effects of seeding treatment, the second row (d–f) shows the effects of the cage treatment, and the third row (g–i) shows the effects of the nurse plant treatment. Asterisk (*) in upper left corner indicates sites with a significant difference in leaf number between treatments (see Table 1).

Table 1. Summary of statistical results for effects of cages, nurse plants, and their interaction at Low Elevation on seedling emergence, growth, and survival.

Low Elevation	Emergence		Growth		Survival	
Treatment Effects	Test Statistic	p	Test Statistic	p	Test Statistic	p
Cage	18.852	< 0.0001	0.287	0.607	17.891	< 0.0001
Nurse plant	9.273	0.002	7.229	0.028	0.084	0.772
Cage*nurse plant	0.365	0.546	0.774	0.405	0.191	0.662

Plots in the seed ball treatment group were omitted. The test statistics given are the likelihood ratio χ^2, F, and log-rank χ^2 for emergence, growth, and survival, respectively. Degrees of freedom = 1 for all tests.

with elevation and depended in part on the cage treatment. At Low Elevation, proximity to creosotebush had positive effects on emergence, irrespective of the cage treatment (Table 1; Fig. 2a), negative effects on leaf growth (Fig. 1g), and no effect on survival (Fig. 4a).

At Mid-Elevation, nurse plant effects on emergence were positive only when cages were present and creosotebush as a nurse plant had a stronger positive effect than blackbrush ($p = 0.046$; Fig. 2b). Without cages, creosotebush had no effect

on emergence, whereas blackbrush reduced emergence compared to plots in the open. Nurse plants did not affect growth (Fig. 1h), but negatively affected survival when cages were absent (Fig. 4b), with creosotebush having the larger negative effect (Table 2).

At High Elevation, nurse plant effects on emergence were negative only outside of cages (Table 3; Fig. 2c). There were no nurse plant effects on growth (Fig. 1i) or survival (Table 3; Fig. 4c).

Table 2. Summary of statistical results for effects of cages, nurse plants, and their interaction at Mid-Elevation on seedling emergence, growth, and survival.

Mid-Elevation	Emergence			Growth			Survival		
Treatment Effects	Test Statistic	df	p	Test Statistic	df	p	Test Statistic	df	p
Cage									
Creosotebush	28.416	1	<0.0001	3.787	1	0.075	49.890	1	<0.0001
Blackbrush	9.979	1	0.002						
No nurse	2.247	1	0.134						
Nurse plant									
Cage, creosotebush	31.983	2	<0.0001	0.310	2	0.739	0.026	2	0.872
Cage, blackbrush	5.259	2	0.022				1.490	2	0.222
No cage, creosotebush	1.356	2	0.243				22.704	2	<0.0001
No cage, blackbrush	5.604	2	0.018				4.599	2	0.032
Cage*nurse plant	22.093	2	<0.0001	1.002	2	0.396	11.865	2	0.003

Plots in the seed ball treatment group were omitted. The test statistics given are the likelihood ratio χ^2, F, and log-rank χ^2 for emergence, growth, and survival, respectively. If interaction effects were not significant, only results for the model lacking the interaction are shown (i.e. cage effect on growth and survival and nurse plant effect on growth).

Table 3. Summary of statistical results for effects of cages, nurse plants, and their interaction at High Elevation on seedling emergence, growth, and survival.

High Elevation	Emergence		Growth		Survival	
Treatment Effects	Test Statistic	p	Test Statistic	p	Test Statistic	p
Cage						
Blackbrush	54.738	<0.0001	6.099	0.039	62.248	<0.0001
No nurse	16.281	<0.0001				
Nurse plant						
Cage, blackbrush	0.258	0.612	0.034	0.858	0.740	0.390
No cage, blackbrush	5.707	0.017				
Cage*nurse plant	5.489	0.019	0.081	0.784	0.124	0.724

Plots in the seed ball treatment group were omitted. The test statistics given are the likelihood ratio χ^2, F, and log-rank χ^2 for emergence, growth, and survival, respectively. Degrees of freedom = 1 for all tests. If interaction effects were not significant, only results for the model lacking the interaction are shown (i.e. cage and nurse plant effects on growth and survival).

Omitting all nurse plant plots, we identified significant site*cage effects on emergence and survival ($p < 0.001$). Emergence was nearly twice as high at High Elevation under cages than in any other site and treatment combination (Fig. 2), and a similar pattern was found for survival (data not shown). Without cages, both emergence and survival were highest at Mid-Elevation ($p < 0.001$).

In the comparison of Low with Mid-Elevation and Mid- with High Elevation, main effects of site on emergence and survival were non-significant. For Low compared with Mid-Elevation, only three-way interactions on emergence ($p = 0.005$) and survival ($p = 0.002$) were significant. For Mid- compared with High Elevation, cage*site effects on emergence ($p < 0.001$) and survival ($p = 0.030$) and site*cage*nurse plant effects on survival ($p = 0.051$) were significant. For both site comparisons, positive nurse plant effects were most strongly expressed under cages at Mid-Elevation. Negative nurse plant effects were most strongly expressed without cages at the higher of the two elevations compared. No significant site interactions existed for leaf numbers.

Status After 2 Years

No seedlings emerged between the second and third spring census, consistent with low precipitation in the winter-spring period of 2011/2012, though seedlings survived at every site. Mid- and High Elevation had more green seedlings, equivalent

to 2 seedlings per plot (excluding seed ball plots), compared to only 0.2 seedlings per plot at Low Elevation (GLM: likelihood ratio $\chi^2 = 58.477$, $df = 2$, $p < 0.0001$). At Mid- and High Elevation, more seedlings were in caged than in uncaged plots (GLM—Mid: likelihood ratio $\chi^2 = 62.157$, $df = 1$, $p < 0.0001$; High: likelihood ratio $\chi^2 = 45.184$, $df = 1$, $p < 0.0001$), and more were in the open than in under nurse plants (GLM—Mid: likelihood ratio $\chi^2 = 7.517$, $df = 2$, $p = 0.023$; High: likelihood ratio $\chi^2 = 5.211$, $df = 1$, $p = 0.022$). There was no difference in average number of leaves per seedling between sites (repeated measures ANOVA: $F = 1.323$, $df = 2$, $p = 0.270$).

Discussion

Our hypothesis that seed balls would facilitate emergence at intermediate elevation was refuted; seed balls predominantly negatively affected emergence. However, in Experiment II, the negative effect of seed balls was reduced, but not eliminated, by using less clay and/or smaller, flatter balls. This was surprising because in both experimental years, climatic conditions were good for germination.

Emergence from seed balls was higher in the second than in the first season, suggesting that long-term exposure to the elements facilitated the breakup of seed balls. Proportional emergence from seed balls was also higher in the second season,
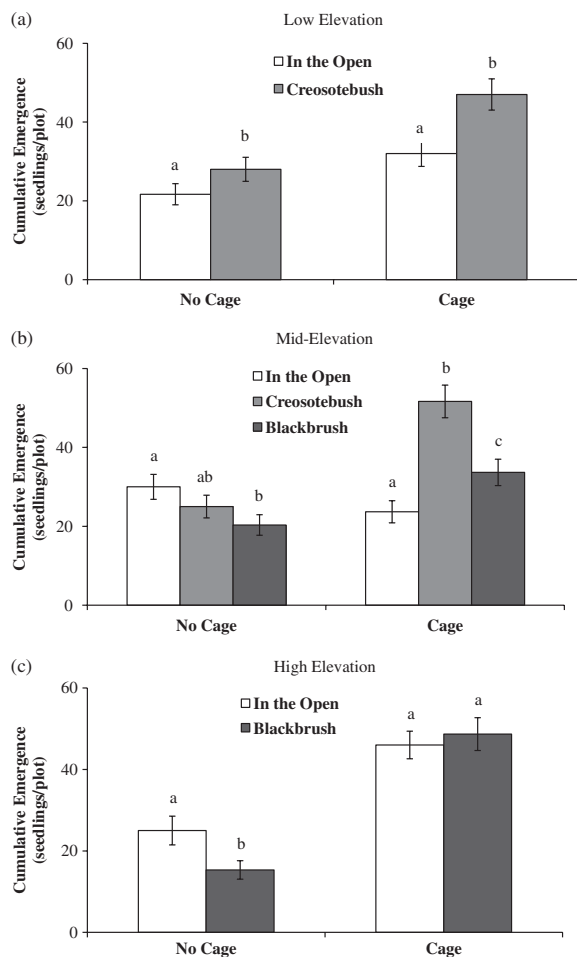
Figure 2. Cage*nurse plant interactions at Low (a), Mid- (b), and High Elevation (c). Mean number of seedlings per plot with standard error bars of the mean are shown. Lowercase letters indicate a significant effect of nurse plant on seedling emergence within the cage treatment.

probably due in part to higher survivorship of seeds inside seed balls. This supports the hypothesis that seed balls can help establish a persistent seed bank. As this study reports mainly on negative effects of seed balls on emergence, the possibility of establishing a perennial seed bank warrants further study. For example, it may be useful to broadcast seed balls in dry years or months ahead of the rainy season without risking the total loss of seeds to predation. That said, overcoming the inhibitory effect of the seed ball even under wet conditions stands out as an important prerequisite for useful application of this technology.

Our second and third hypotheses that the positive effects of cages should increase with elevation, and nurse plant effects decrease, were both supported. Interactions with the cage treatment suggested that nurse plant effects on emergence and survival were mediated by two opposing forces switching dominance along the elevation gradient: environmental conditions becoming more favorable with increasing elevation and predation pressure becoming stronger. The positive environmental effects of nurse plants (observable when predators were excluded) grew weaker with elevation whereas the negative effects of predation (observable by comparing caged and uncaged treatments) grew stronger. Thus, overall nurse plant effects went from positive at Low Elevation to negative at High Elevation.

This result is in accordance with the stress-gradient hypothesis (Bertness & Callaway 1994), but we also observed an effect due to nurse plant identity. At Mid-Elevation, without cages, creosotebush had a stronger positive effect on blackbrush emergence than blackbrush itself, although subsequently, both species depressed survivorship and creosotebush more so than blackbrush. Thus, creosotebush may have created a more beneficial microenvironment for the earliest stages of germination and emergence, perhaps by casting a longer shadow and having wider zone of increased fertility (Whitford et al. 1997), but at the same time, afforded less protection from predation. This refuted our fourth hypothesis that heterospecific nurse plants could reduce predation pressures on seeds and seedlings.

Cages nearly always had a positive effect on seedling emergence, growth, and survival, and the effect increased with elevation. This indicates that predation pressure from rodents was higher inside the core blackbrush community and fits the pattern of higher consumption with increasing plant productivity in relatively unproductive environments (Price et al. 2000; Eskelinen 2008). At Mid- and High Elevation, cage effects were stronger under nurse plants than in the open, suggesting that when predation pressure is higher, it is also more concentrated under shrubs (Longland 1991). Mast seeding, a predation defense mechanism (Kelly 1994), is a further indication that blackbrush is especially exposed to seed and seedling mortality by predation (Meyer & Pendleton 2005).

From the standpoint of restoring burn areas, an encouraging result from this study is that nurse plants are not always required for successful plant establishment; in fact, their long-term effect may be negative. In our experiment, without cages, 2-year-old seedlings were twice as likely to be in vegetation gaps than under nurse plants. As top-down predation effects increase when bottom-up stress effects are relaxed, that is in "good" years (Vince et al. 1981; Smit et al. 2009), we expect to see proportionally more recruitment away from vegetation than in densely vegetated areas that attract foragers (Parmenter & MacMahon 1983).

Cages are obviously very effective for deterring rodents, but they are also costly to implement. This cost should be weighed against increases in establishment, which in our experiment was on an order of magnitude. Therefore, exclusion cages could have a role in establishing pioneer shrubs that would eventually supply seeds to establish a self-sufficient population.

A long-lived shrub such as blackbrush typically takes decades to mature (S. Meyer 2012, USFS, Provo, Utah, personal communication). This is a time scale over which changes in local climate could be profound. The range of blackbrush has responded to climate fluctuations over the past 12,000 years, expanding into lower elevations during colder periods and contracting upwards during warmer periods (Hunter & McAuliffe 1994).
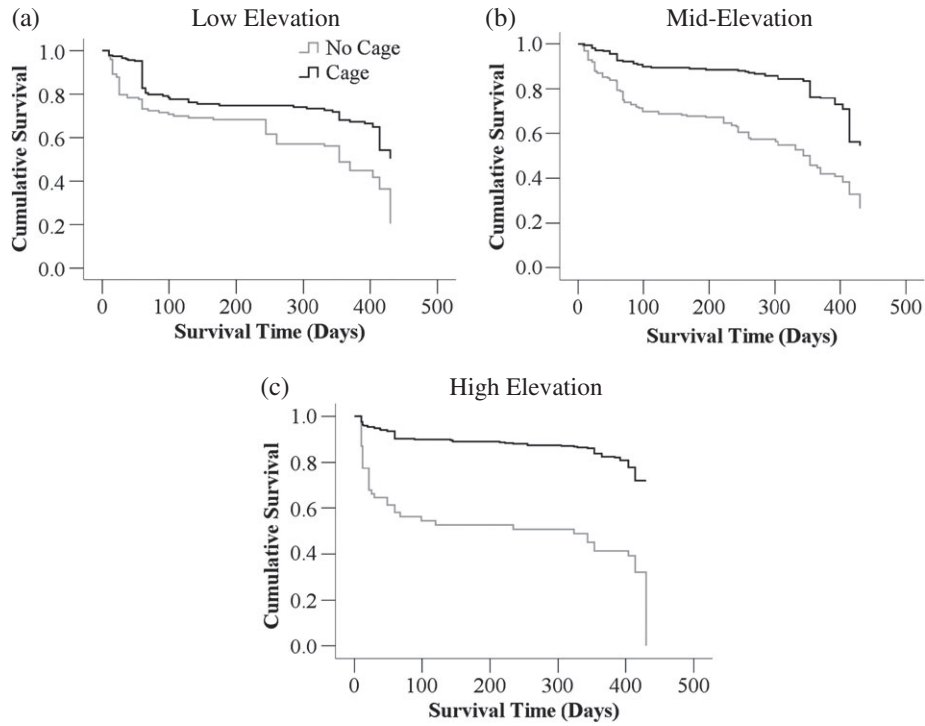
Figure 3. Kaplan–Meier seedling survival curves at Low (a), Mid- (b), and High (c) Elevation for cage effect. Cages significantly increased survival at all sites, with the strongest effect at High Elevation (log-rank test—Low vs. High Elevation: $\chi^2 = 14.89$, $p < 0.001$; Mid- vs. High Elevation: $\chi^2 = 5.98$, $p = 0.015$; Low vs. Mid-Elevation: $\chi^2 = 3.18$, $p = 0.075$).
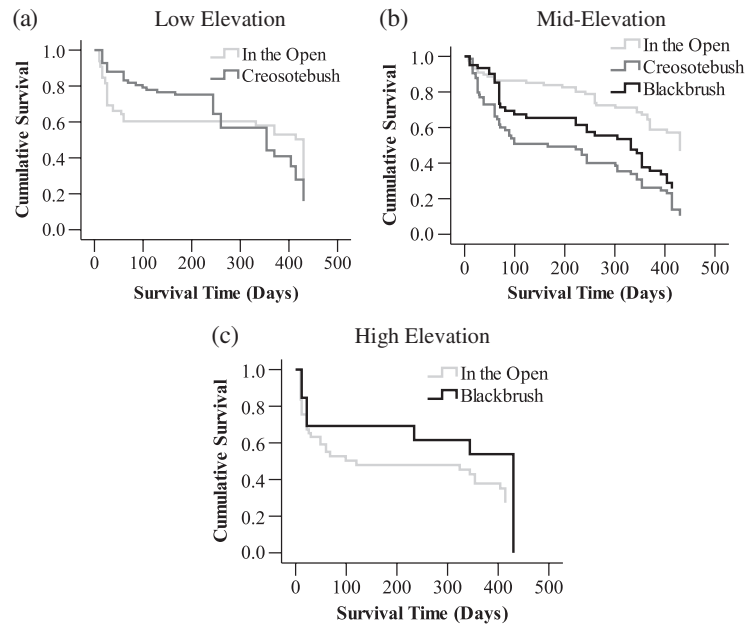

Figure 4. Kaplan–Meier seedling survival curves at Low (a), Mid- (b), and High (c) Elevation for plots without a cage. Nurse plants did not significantly affect survival at Low or High elevation (See Table 1). At Mid-Elevation, survivorship was highest in the open and lowest under creosotebush (log-rank test—in the open vs. creosotebush: $p < 0.001$; in the open vs. blackbrush: $p = 0.001$; creosotebush vs. blackbrush: $p = 0.046$).

Assuming the climate in the Mojave will continue warming (Hereford et al. 2004; Seager et al. 2007), it is likely that the poor recruitment observed at Low Elevation will soon be typical for higher elevations as well. Interestingly, during 2 years of our experiment, the three sites differed chiefly in temperature and soil moisture, not rainfall. This suggests that warming alone, even without a decrease in average precipitation, can inhibit blackbrush recruitment. An additional concern is the influx of invasive grasses, which may be facilitated by the nurse plant effects of native shrubs (Abella 2009). This has compelled some to suggest that restoration of certain native shrubs is an exercise in futility (Abella & Smith 2013). However, we suspect that the interactions of native shrubs and invasive grasses, as well as their responses to fire, are also subject to modification along the elevation gradient, and that blackbrush communities may continue to be viable at higher elevation.

Implications for Practice

- Seed coat preparations (e.g. seed balls) increase seed survivorship but may also reduce germinability. Understanding species-specific costs and benefits of this restoration practice is important because preparation costs can be prohibitive and not defensible if establishment success is minimal.
- Designing nurse plant cover for restoration can be beneficial in the most stressful portions of species' ranges (e.g. drier and/or expected to shift to harsher environmental conditions). However, they may not be advisable in core habitat areas where nurse plants attract predator foraging.
- If restoration specialists/managers determine that engineering nurse plant cover is necessary in core habitats, then predator exclusion cages may be required to achieve plant establishment goals for some species.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Cumulative precipitation (a), average volumetric soil water content at 10 cm (b) and 30 cm (c) depth, average soil temperature at 10 cm (d) and 30 cm (e) depth at three study sites. A second replicate of all probes was added to each site on 20 July 2010. Data loss for Mid- and High Elevation sites occurred from 7 October to 22 November 2010.