

SEEDLING ECOLOGY AND RESTORATION OF BLACKBRUSH
(*COLEOGYNE RAMOSISSIMA*) IN THE MOJAVE DESERT

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SEEDLING ECOLOGY AND RESTORATION OF BLACKBRUSH
(*COLEOGYNE RAMOSISSIMA*) IN THE MOJAVE DESERT

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ABSTRACT

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by

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Worldwide, ecological communities are disappearing due to the joint stresses of climate change, species invasions and urbanization. In the southwestern U.S., the blackbrush (*Coleogyne ramosissima*) community is among the most threatened. It occurs primarily in the transition zone between the Mojave and Great Basin deserts and on the western border of the Sonoran Desert, forming vegetation bands at mid-elevation between 750 and 1,900 m from southeastern California to southwestern Colorado. Fire is the most important threat to this community, as blackbrush is slow to regenerate after fire, and fire frequency has increased due to global warming and invasion by exotic grasses, which added fine fuels. The blackbrush community could disappear entirely in the foreseeable future if steps are not taken to facilitate shrub regeneration after fire.

In this study, I tested the efficacy of several methods for promoting the germination and establishment of introduced seeds, each designed to mitigate potential recruitment bottlenecks: lack of sufficient moisture, seed and seedling predation, and high incident radiation. In addition, I tested these methods across an elevational gradient,

to determine if best practices differ by location in the blackbrush range. I hypothesized that a) negative effects of moisture limitations and b) positive effects of proximity to nurse plants would decrease with elevation, while c) rates of seed or seedling predation would increase with elevation as plant productivity and rodent food availability increases.

I conducted two plot-scale experiments over two years in the Mojave Desert of southern California using a fully factorial design at each of three elevations. Factors included a) seed preparation (encapsulated in seed ball to trap moisture surrounding the seed, or bare seed), b) predator-exclusion (with or without wire cages), and c) proximity to mature shrubs (distant or near). Three elevations were chosen on the basis of local blackbrush abundance from low, at the lower boundary of its range, to high in the zone where blackbrush begins to exclude most other shrub species.

In the two years of the study, across sites and treatments, germination from bare seeds was much higher than from seed balls. Emergence and survival were highest in caged plots across the elevational gradient, and effect sizes increased with elevation. There was a positive effect of creosotebush nurse plants on emergence at low elevation, while proximity to a nurse plant interacted with the cage treatment mid- and high elevation such that there was higher predation under adult shrubs even though they provided a beneficial micro-climate in the presence of predator exclusion cages. Supporting my initial hypotheses, blackbrush regeneration was most limited by predation at the highest elevation, while positive nurse plant effects were maximized at lowest elevation. However, encapsulation of the seed had negative effects in the first growing season but permitted seeds to persist in the seed bank into the second growing season, creating a bet hedging strategy not naturally present in this species. More large seedlings were present at mid- and high elevation.

Blackbrush recruitment in the Mojave Desert depends on rare year types with higher than average precipitation and effective restoration has to take rainfall uncertainties into consideration. Use of seed balls may help blackbrush maintain a seed bank, which could be more important for achieving establishment than achieving high germination rates using bare seeds only in the year of application. Proximity to nurse plants should be a minor consideration, as the environmental benefits of germinating close to a mature shrub are partially or fully outweighed by predator attraction. My study

shows that the careful examination of a species' vulnerabilities and conditions for recruitment can help formulate sensible strategies for restoration and can be used as a model for the restoration of other threatened plant communities in a variety of contexts.

CHAPTER I

Introduction

The Global Threat to Shrubland Communities

Shrub communities are under threat worldwide because of global climate change, changes in fire regimes, species invasions, and urban encroachment (McDonnell and Pickett 1990, Schwartz et al. 2006). Climate, fire, and vegetation are interconnected such that a change in one will affect the others (Ryan 1991). Due to climate change, major shifts in vegetation zones are expected in many regions, thereby altering the structure and composition of plant communities and affecting fire potential by changing the physical and chemical properties of fuels (Ryan 1991).

In the desert, shrub regeneration is rare, since they are physiologically adapted to maintenance of long-lived individuals at the expense of reproduction, and regeneration frequently relies on masting events based on sufficient spring precipitation (Lovich and Bainbridge 1999, Shreve 1942). In the extreme desert environment, plant growth and establishment are naturally slow and disturbance exacerbates these conditions (Lovich and Bainbridge 1999). Conditions suitable for plant establishment occur only infrequently and irregularly, and it may take hundreds of years for full recovery to take place without active intervention (Lovich and Bainbridge 1999). The invasion of the non-native, annual grass cheatgrass (*Bromus tectorum*) to Intermountain West sagebrush

shrublands has elevated wildfire frequency from a 30-110 year historical cycle to as much as every three to five years today, reduced native plant and animal biodiversity, deteriorated agricultural land and rangelands, and required large financial expenditures for fire suppression (Belnap et al. 2003, Chambers et al. 2007). Positive feedback between *B. tectorum* colonization and shrub decline through the accelerated fire cycle, has made the conversion of shrublands to annual exotic grasslands very rapid (D'Antonio and Vitousek 1992).

One of the most threatened shrubland biomes in the southwestern U.S. is the blackbrush (*Coleogyne ramosissima*) community, which occurs primarily in the transition zone between the Mojave and Great Basin deserts and on the western border of the Sonoran Desert, forming a relatively narrow band (covering three million hectares) at mid-elevation between 750 and 1,900 m from southeastern California to southwestern Colorado (Meyer and Pendleton 2005, Pendleton and Meyer 2004). Despite spanning a relatively limited geographic extent, blackbrush occupies a range with steep climate gradients. It is associated with generally shallow, poorly developed soils that often have abundant exposed rock and high sand content (Anderson 2001, Callison and Brotherson 1985), including rocky slopes (Beatley 1976, Shreve 1942, West 1983). Because of its higher tolerance to freezing, blackbrush can grow where other desert perennial shrubs cannot. The blackbrush community thus serves important ecological functions by providing quality habitat for animal species (Brooks and Matchett 2003, Shreve 1942), protecting the soil from erosion, providing shelter for seedlings from high radiation exposure and enriching soil fertility. Blackbrush helps to retain nitrogen in the ecosystem by storing it in roots, leaves, and stems (Anderson 2001) and, by altering the soil

chemistry, it increases nitrogen and phosphorus availability beneath its canopies compared to interspaces among shrubs (Anderson 2001, Bowns 1973). In addition, the soil under blackbrush has consistently higher moisture content than white bursage (*Ambrosia dumosa*) and creosotebush (*Larrea tridentata*) and it retains greater soil moisture into the dry months (Brittingham and Walker 2000).

Climate in the deserts of the western United States is predicted to get hotter and drier, and blackbrush communities are located in regions of greatest change (so called “hot spots”; Kerr 2008, Seager et al. 2007). Analysis of packrat middens showed that the blackbrush community expanded and contracted along elevational gradients over the past 12,000 years due to climate fluctuations (Cole and Webb 1985, Hunter and McAuliffe 1994, Van Devender 1990). In the Mojave Desert, blackbrush is thought to be already on the trailing edge of its lower elevational distribution, and at the limit of its capacity to recruit (Meyer and Pendleton 2004). The magnitude of the temperature increases predicted for the Mojave Desert, especially the trend towards warmer winters (Meyer and Pendleton 2005), may still further reduce its present range (Abella 2009). Further, if the climate trend continues, it is predicted that recruitment success will be greater in habitats at higher elevations and latitudes throughout its range (Meyer et al. 2005).

Hotter and drier conditions will also increase drought and fire frequencies (Littell et al. 2009), both risk factors for blackbrush, which is drought deciduous and not adapted to fire. Blackbrush’s resinous leaves are easily ignited and where blackbrush density is high, fire can spread quickly (Callison et al. 1985). Recovery from fire damage is slow since the shrubs do not resprout, seed production is infrequent, rates of seed and seedling predation high, and moisture requirements for successful recruitment are also high,

excluding recruitment in all but the wettest years (Pendleton and Meyer 2004). It may take 60 years or more for the blackbrush community to reach a climax state after fire (Anderson 2001). Exotic grasses typically invade long before a climax state is reached, and this starts a fire cycle that ultimately prohibits the return of the blackbrush community (Brooks and Matchett 2006, Brooks et al. 2007).

Without human mitigation, if current trends of climate change and exotic grass invasion continue, blackbrush communities in the western US, particularly the Mojave Desert, may be permanently lost (Webb et al. 2003). Thousands of acres of blackbrush have already been destroyed in the Mojave Desert due to fire and other disturbances (T. Esque, personal communication). Therefore, a high-priority conservation goal is to develop procedures that accelerate the re-establishment of blackbrush after large-scale disturbance.

Blackbrush Recruitment

Long-lived desert shrubs, such as blackbrush, have a life history strategy of emphasizing maintenance of existing individuals at the expense of reproduction (Webb et al. 1987). Blackbrush produces occasional mast seed crops when environmental conditions are favorable, followed by several years of minimal seed output (Pendleton and Meyer 2004, Pendleton et al. 1995). Winter precipitation initiates flowering, but the size of the fruit crop is a function of available stored resources (Anderson 2001, Pendleton and Pendleton 1998). In most years, nearly all seeds are consumed by rodents and seedling mortality is also high due to predation by rodents and limited soil moisture (Lovich and Bainbridge 1999, Monsen et al. 2004, Pendleton and Meyer 2004, Pendleton

et al. 1995). Significant recruitment usually follows only mast years (Meyer and Pendleton 2005). Seeds require heavy, early spring rains to germinate, which is an unpredictable and rare event in the Mojave Desert (Anderson 2001, Meyer and Pendleton 2005, Pendleton et al. 1995). Recruitment in mature blackbrush stands is also low due to competitive suppression of seedlings by adults, and occurs most commonly in small canopy gaps created by local-scale disturbances (Meyer and Pendleton 2005).

The primary challenge for blackbrush restoration is to accelerate the naturally low rates of recruitment. This would lower the risk that former blackbrush stands become replaced by exotic grasses (primarily red brome (*Bromus rubens*) and cheatgrass). Accelerated recruitment requires an increase in seed abundance, high rates of germination, especially in wet years when the chance for seedling survival is higher, and rapid seedling growth. The high abundance of seeds is important to counter high seed and seedling predation rates in any year. However, high predation rates are irrelevant if all seedlings eventually die through exposure to the harsh summer environment. Therefore, equally important to seed addition maybe the creation of a more stable seed bank, so that seeds are available for germination in the rare wet year. In addition, it is desirable that in such rare wet years, seedlings should grow fast, so that by May, their root systems are sufficiently deep to maintain contact with the receding soil moisture.

A number of restoration techniques have been developed to counter the negative effects of seed and seedling predation, a harsh micro-environment, as well as moisture uncertainty. These include the broadcasting of seeds inside seed balls, the use of predator exclusion cages, and the planting of seeds under nurse plants.

The seed ball method was formally introduced to the West in Masanobu Fukuoka's book on natural farming "The One-Straw Revolution" (1978), and has since been used by researchers and professionals in both agriculture and restoration contexts, though there has been little scientific study of how seed balls work and their effect on shrub establishment. Aside from allowing convenient dispersal since they can be made in advance and do not have to be buried, it is hypothesized that this procedure eliminates seed predation by wildlife and helps to retain moisture around the seeds to promote germination.

In deserts, removal of seeds by rodents and harvester ants may severely limit seedling establishment (Lovich and Bainbridge 1999, Reichman 1979). Predator exclusion cages address threats from granivory and herbivory to increase seedling germination and survival. The blackbrush seed is too large for predation by ants, but they are a preferred food of heteromyid rodents (J. Auger, University of Nevada, Reno, unpublished data). These rodents are also the primary dispersers by creating scatter hoards, surface seed caches, which either are later eaten as seeds, grazed upon as young sprouts soon after emergence, or forgotten (Meyer and Pendleton 2005). Predation pressure increases with elevation in the Mojave because higher productivity allows for a higher abundance of rodents or the presence of larger rodents that have higher metabolic requirements (Price et al. 2000). Rodent abundance also varies in time, dependent on precipitation effects on productivity (Stapp and Polis 2003). Rodent abundance tends to peak about one year after productivity peaks, which may give seedlings a one-year window of opportunity for escaping predation (Ernest et al. 2000, Ostfeld and Keesing 2000, Previtalli et al. 2009, Shenbrot et al. 2010, Thibault et al. 2010, Whitford 1976).

In the harsh environment of the desert, recruitment of perennial plants most often occurs within the protected microhabitats of established shrub canopies (Brittingham and Walker 2000, Niering et al. 1963, Raffaele and Veblen 1998). Desert shrubs create fertile islands which become the center of a lengthy process of colonization and succession where nutrient cycling, plant productivity, and animal activities are all higher compared to intershrub spaces (Longland and Bateman 2002, Thompson et al. 2005, Walker et al. 2001). These “nurse plants” provide a more benign micro-environment that facilitates germination (Shreve 1925). The survival of seedlings beneath a nurse plant plays an important role in structuring vegetation (Brittingham and Walker 2000). The effects of proximity to adult shrubs have been shown to be modified by aridity as well, with facilitative effects increasing and competitive effects decreasing with aridity, and vice versa (Holmgren et al. 1997).

Since blackbrush occupies an elevational range encompassing a wide array of precipitation and temperature conditions, different factors may limit recruitment at different elevations. This suggests that not all restoration techniques are equally effective everywhere in the blackbrush range. For example, moisture at the soil surface evaporates most rapidly at lower elevations, where it is hotter and drier, therefore, techniques that retain soil moisture for longer may be effective, but they may not have the same impact at high elevation, where moisture is naturally retained for longer. Conversely, because of the higher plant productivity, and presumably higher rodent density, predator exclusion cages may be more effective at higher elevation. Nurse plant effects should be more pronounced at the lower elevational end of the blackbrush range where conditions are hotter and drier.

Study Goals

My overall research objective was to develop community-specific blackbrush restoration techniques aimed at accelerating the re-establishment of the blackbrush community after disturbance. My strategy was to evaluate the need to control three factors that could potentially lower establishment success: soil moisture retention surrounding the seed, seed and seedling predation, and microclimate. I expected the influence of each of these factors to change with elevation, therefore I repeated my experiment at three locations within the blackbrush elevational range: at one site where blackbrush is a minor community component (less than 0.1% cover) at low elevation, one site at mid-elevation where blackbrush co-dominates with other shrubs (0.3% blackbrush cover), and one site well within the blackbrush belt (20% cover).

Hypotheses

My hypotheses are graphically illustrated in Figure 1.

1. Effect of seed balls: I expect seed balls to increase emergence rates because of reduced seed predation and because the clay will retain moisture for longer and thereby stimulate germination. Within the seed ball treatment, I would expect emergence to be highest at the intermediate elevation, because at lower elevation, seed balls may not provide enough of an effect to overcome the overall drier conditions, whereas at higher elevation there may be enough soil moisture even in the absence of seed balls. With improved emergence from seed balls, I expect survival and seedling growth to benefit.

2. Effect of exclusion cages: I expect cages that exclude rodent predators to increase seedling emergence, growth, and survival, with the strongest positive effect at the highest elevation where productivity, and presumably local herbivore abundance, is highest.
3. Effect of proximity to adult shrub: I expect that the more benign micro-environment on the north side of adult shrubs will increase emergence, growth, and survival at the lowest elevation where heat exposure at ground level is highest. However, the effect may become neutral or even negative with increasing elevation, as the effect of improved micro-climate on emergence, growth, and survival weakens and/or competitive effects of the adult on the seedling increase.

Methods

Study Site

The study site was located on Bureau of Land Management (BLM) land in the southern Mojave Desert of Mountain Pass, California, near the Mojave National Preserve (BLM permit 6524 610.21). Three experimental sites span an elevational gradient of approximately 250 m along a gently sloping bajada (Figure 2). At the lowest elevation at 1,260 m, creosotebush is the dominant species, yucca (*Yucca* spp.), cacti (*Opuntia* spp.), and wolfberry (*Lycium andersonii*) are common, and blackbrush is comparatively rare. The soil at this site is over 1 m deep. At mid-elevation at 1,305 m, the soil is about 65 cm deep and is situated within a wide transition zone with about equal cover of creosotebush and blackbrush, and a high abundance of yucca, cacti, and white ratany (*Krameria grayi*). At the highest elevation at 1,510 m, the soil is about 30 cm deep with a typical blackbrush-dominated community with only isolated individuals of creosotebush, Mojave

yucca (*Yucca schidigera*), and banana yucca (*Yucca baccata*). These sites were selected to cover the range of the blackbrush community in this area, from low blackbrush density to high density.

The mean annual temperature for Mountain Pass is 14.4° C (53 years on record) with summer and winter average extremes of 33.8° C and -1.4° C (Weatherbase 2010). The average yearly precipitation for Mountain Pass is 212 mm (53 years on record; Weatherbase 2010).

Experiment 1

This experiment was started between January 30 and February 1, 2010. The experimental design was a balanced, fully factorial three-factor design with two levels (or treatments) for each factor resulting in eight treatment combinations (2 x 2 x 2), each represented by three replicates at each site (Figure 2, Table 1). The mid-elevation site had a third treatment for the third factor, or a 2 x 2 x 3 design (Table 1). Seeds were purchased from Comstock Seed in Gardnerville, NV, and were certified to have 93% viability. The experimental unit was a plot of 70 cm by 70 cm that each received a total of 150 seeds. Three seeds were dropped into each of 50 holes and immediately covered by soil. Holes were arranged in a regular lattice pattern and were about 1-2 cm deep. Plots were unmarked to avoid drawing the attention of wildlife and humans, except for a rebar inserted into the northwest facing corner of each uncaged plot. The exact location of each plot was captured by its GPS coordinates.

Seeds were either applied directly (buried 1-3 cm below the surface) or encapsulated inside seed balls (half-buried so that the seeds inside were at a depth

equivalent to those applied directly; Factor 1). The soil mixture followed the recipe by Hoines and Edwards (2009). The mixture contained 28 units Miracle Grow organic garden soil, 11 units dry red art clay, 11 units coconut fiber, 5 units leveling sand, and enough water to make the soil mixture moldable and hold form. Each seed ball was approximately 3-4 centimeters in diameter and was seeded with three blackbrush seeds in the center. Seed balls were air dried immediately to avoid premature germination. After several days of drying they had hardened and could be packed and transported with minimal disintegration.

Herbivore exclusion cages were erected immediately after seeding (Factor 2). Cages were 80 cm long and wide, 30 cm deep, and open at the bottom. They were made from galvanized steel hardware cloth with 1.25 cm mesh size. To discourage rodents from burrowing into the cages, they were partly buried, so that the top was 10-15 cm above the soil.

Half of the seed plots were positioned on the north side of a mature shrub, as close to the main stem as possible, to establish a nurse plant treatment, with the control treatment established at least 1 m away from the nearest shrub (Factor 3). The shrub species chosen varied with site depending on species abundance: creosotebush served as nurse plant at the lowest elevation, both blackbrush and creosotebush at intermediate elevation, and blackbrush at the highest elevation.

Thus, the total number of plots was 24 at the highest and lowest elevations ((+/- nurse plant) * (+/- cage) * (+/- seed ball) * replication 3), and 36 at intermediate elevation (creosotebush nurse/blackbrush nurse/no nurse plant) * (+/- cage) * (+/- seed ball) * replication 3). The treatment combination for each plot was chosen randomly,

constrained only by the spatial distribution of the respective nurse plants. In error, at the high elevation site, there was one additional caged plot and a missing uncaged plot.

Experiment 2

Because of extremely low emergence from the seed ball treatment in experiment 1, I conducted a second, shorter-term experiment to test other seed ball recipes. This experiment was started on November 23, 2010. I speculated that emergence failed for seed balls in the first experiment because too much clay may have prevented seed balls from becoming fully inundated and breaking apart for the growing seed. Blackbrush generally grows well on sandy to loamy substrates and poorly on clay (Korthuis 1988). Therefore, for this experiment, I tested two new seed ball recipes, both with less clay. I also made the seed balls smaller (3 cm diameter) and flattened them to increase surface area.

Recipe 1 contained 9 units Miracle Grow organic garden soil, 2 units dry red art clay, 2 units coconut fiber, 4 units leveling sand, and enough water to make the soil mixture moldable and hold form. Recipe 2 contained 16 units soil, 4 units dry clay, 1 unit coconut fiber, 4 units sand, and a little water. As before, each seed ball was seeded with three seeds.

The plot design and site locations were as before, however, I simplified the experimental design to focus on the effect of seed balls on emergence (Hypothesis 1), Thus, I eliminated the cage and neighbor treatment, while increasing the replication number to four.

Tracking Emergence and Survivorship

Seedlings were censused every 7-22 days in the spring of 2010 (experiment 1) and in March, April, and May 2011 (experiment 2). From May 31 to August 12, 2010, plots were censused weekly or every other week. I defined emergence as the appearance of the seedling above ground. The census protocol was to identify all newly emerged seedlings in a plot by coordinate location and to mark them by placing wire loops around them or inserting toothpicks close to them to make it easier to find them in subsequent censuses. Toothpicks were color marked to identify the dates seedlings were first recorded. Additionally, the new seedlings' heights and leaf numbers were recorded. At the same time, the presence and absence of previously emerged seedlings (identified by location and toothpick color) were also recorded, as well as their heights and leaf numbers.

I also occasionally searched for naturally emerged seedlings outside of seeded plots, in areas the same size of plots and using the same search effort. Neither in the open nor close to shrubs, did I ever find a naturally emerged seedling, suggesting that I could ignore the possibility of germination from the seedbank.

Precipitation, Soil Moisture, and Soil Temperature

To capture site differences in rainfall and soil moisture dynamics between sites, I installed a precipitation and soil moisture monitoring system at each site. Each system was equipped with a rain gauge (EcH₂O Rain model ECRN-50, Decagon Devices Inc., Pullman, WA, USA) and 4 soil moisture and temperature probes (EcH₂O EC-TM, Decagon Devices Inc., Pullman, WA, USA), with 2 probes each placed at 10 cm and 30

cm below the surface. A second monitoring system was installed at all sites on July 20, 2010. The sensors were connected to two battery powered data loggers (Em50 EcH₂O logger, Decagon Devices Inc., Pullman, WA, USA) using a logging interval of 15 minutes. Soils were quite similar across sites and composed of mostly sand and gravel.

Vegetation Assessment

To characterize the vegetation differences at the three experimental sites, I determined perennial shrub and stem succulent density and ground cover by the belt transect method (Bonham 1989). At each site, four belt transects of 50 m length and 1 m width were surveyed in the spring of 2010. Perennial shrub and stem succulents were counted by species, and their location along the length of the transect was recorded as well as their canopy diameter. The three dominant perennial species at each site, plus blackbrush and creosotebush as indicator species, are reported in Table 2. Creosotebush density decreased and blackbrush density increased with increasing elevation.

Canopy and ground cover were measured along the boundary lines of the belt transects using the line intercept technique (Bonham 1989). The canopies of all perennial shrubs and stem succulents intercepting the line were recorded by species, height of the cover, and the start and end points of the intercept. Other cover categories were assessed, including bare soil, gravel, rock, bedrock, and litter. Any canopy or ground cover type of 5 cm or less in intercept length was ignored as was any gap in a single cover type of 10 cm or less. Cover of live and dead portions of a single plant were differentiated. The three dominant perennial species with the greatest percentage of total plant cover for each site,

plus blackbrush and creosotebush, are reported in Table 3. Creosotebush cover decreased and blackbrush cover increased with increasing elevation.

Statistical Analysis

Emergence and Survivorship

Because emergence is generally a rare event, I assumed the Poisson distribution for cumulative emergence in a generalized linear model in SPSS v.19 (IBM Corporation, Armonk, NY, USA) to compare differences between treatments within and among sites. I conducted a log-rank test to determine significant treatment effects on seedling survival using Kaplan-Meier survival functions which analyze length of seedling survival via a time-to-event approach, where seedling death is the event. I was conservative in my classification of seedling mortality since seedlings could retain living material below-ground even if the above-ground plant did not appear living. As such, a seedling was deemed dead only when it could no longer be located.

Seedling Density

Factors affecting seedling density per plot across all three sites on the last census date (May 11, 2011) were compared using a Poisson distribution in the generalized linear model analysis in SPSS.

Seedling Growth

Indicators of growth (average height and leaf number) of seedlings were analyzed by repeated measures ANOVA in SPSS.

Results

Experiment 1

Precipitation, Soil Moisture, and Soil Temperature

Cumulative precipitation across the three sites from February 1, 2010 to October 6, 2010 showed little difference in total precipitation along the elevational gradient (Figure 3). Due to data loss at stations at mid- and high elevation from October 7 to November 23, 2010, cumulative precipitation was likely underestimated at these sites and the precipitation difference of up to 16 mm seen between sites at the end of the year are likely overestimates. Soil moisture at 10 and 30 cm depth was lowest at the low elevation site and highest at high elevation (Figure 3). Moisture was generally higher with more day to day variability at 10 cm compared to 30 cm and there was more differentiation between sites at the deeper depth. Soil temperature at 10 and 30 cm depth was similar at the two lower sites, but generally cooler at high elevation during the summer months only (Figure 3). Soil temperature at 10 cm depth was typically warmer than the temperature at 30 cm depth during the summer.

Emergence

Between the February 1, 2010 seeding date and March 7, 2010, when the first census was conducted, 40 mm of rain or snow were recorded at the rain gauges (Figure 3). The cold and wet weather continued through the end of April, allowing for more seedling emergence until May 11, 2010. Seedlings emerged first at the lower two elevations and last at high elevation, although seedlings at the highest elevation eventually reached higher cumulative emergence rates (Figure 4).

In the first growing season (March 7, 2010 to November 22, 2010), 8.4% of all sown seeds emerged. A new cohort of seedlings emerged in spring 2011, which by the last census date on May 11, 2011, added 599 more seedlings, or 5.2% of seeds that had not emerged as of November 22, 2010. For the entire study period, 13.1% of all sown seeds emerged. Relatively more seedlings emerged in the second year at the two lower elevations, so that by May 2011, there was no significant difference in total emerged seedlings among sites (Likelihood ratio $\chi^2=5.050$, $df=2$, $p=0.08$).

Seed Ball Effects (Hypothesis 1)

Emergence from bare seeds was much higher than from seed balls across elevations (Figure 5). Across sites and treatments, total emergence from March 7, 2010 to May 11, 2011 was 1,365 seedlings for bare seeds (83% of total emergence) and 288 for seed balls (17% of total emergence). The mid- and high elevation sites had significantly higher emergence from seed balls compared to the low elevation site (Likelihood ratio $\chi^2=83.825$, $df=2$, $p<0.001$; Figure 5), though this was mostly driven by higher seed ball emergence in the second cohort (March-May 2011). Over the elevational gradient that I tested, emergence from seed balls increased with elevation, though again, this trend was driven by the seed ball emergence in the second growing season.

More importantly, seed balls delayed emergence relative to bare seed. Cumulative emergence reached the halfway mark 11 days later, on average, from the seed balls compared to bare seed. During the first growing season, 3.1% of the cumulative emerged seedlings were from seed balls. However, during the second growing season, 42.6% of the cumulative emerged seedlings were from seed balls. For the second cohort, 11%,

50%, and 61% of total emerged seedlings came from seed balls at the low, mid-, and high elevation sites respectively.

At low and mid- elevation, seedlings planted as bare seed were taller and had more leaves compared to those from seed balls (Figure 6; repeated measures ANOVA: low elevation: height: $F=38.523$, $df=1$, $p<0.001$; leaves: $F=25.569$, $df=1$, $p<0.001$; mid-elevation: height: $F=42.257$, $df=1$, $p<0.001$; leaves: $F=21.319$, $df=1$, $p<0.001$). Direct seed application was better for plant growth compared to using seed balls at these elevations, but had no effect at high elevation (Figure 6; repeated measures ANOVA: height: $F=0.344$, $df=1$, $p=0.566$; leaves: $F=0.067$, $df=1$, $p=0.799$).

Because of the low emergence rate from seed balls, and to simplify the interpretation of cage and nurse plant effects, I excluded the seed ball treatment from all subsequent analyses.

Cage Effects (Hypothesis 2)

Cages positively affected emergence across the elevational gradient (Figure 7; low elevation: Likelihood ratio $\chi^2=18.852$, $df=1$, $p<0.001$; mid-elevation: Likelihood ratio $\chi^2=13.973$, $df=1$, $p<0.001$; high elevation: Likelihood ratio $\chi^2=66.231$, $df=1$, $p<0.001$).

Cages significantly increased seedling survivorship at all three sites (Figure 8; Log-rank test: low elevation: $\chi^2=17.891$, $p<0.001$; mid-elevation: $\chi^2=49.840$, $p<0.001$; high elevation: $\chi^2=64.248$, $p<0.001$).

Without cages, there were no differences in survival between sites. With cages, survival was highest at the high elevation site and lowest at the low elevation site (Figure

8; Log-rank test: low v. high elevation: $\chi^2=14.888$, $p<0.001$; mid- v. high elevation: $\chi^2=5.975$, $p=0.015$; low v. mid-elevation: $\chi^2=3.178$, $p=0.075$).

Cages also improved seedling growth at mid- and high elevation, with no difference in emergence date for caged and uncaged plots. Though at mid-elevation, the effect of cages on height was marginally significant, with stronger differences observed later in the study period (Figure 9; repeated measures ANOVA: mid-elevation: height: $F=3.894$, $df=1$, $p=0.060$; leaves: $F=7.686$, $df=1$, $p=0.011$; high elevation: height: $F=5.079$, $df=1$, $p=0.040$; leaves: $F=9.110$, $df=1$, $p=0.008$).

Nurse Plant Effects (Hypothesis 3)

Nurse plant effects were not uniform across sites, and they were different for creosotebush and blackbrush as nurse plants. Creosotebush nurse plants positively affected emergence at low and mid-elevation (Figure 10; low elevation: Likelihood ratio $\chi^2=9.273$, $df=1$, $p=0.002$; mid-elevation: Likelihood ratio $\chi^2=11.314$, $df=2$, $p=0.003$). Blackbrush nurse plants had no effect on emergence at mid-elevation, while they had marginally significant negative effects at high elevation (Figure 10; Likelihood ratio $\chi^2=3.465$, $df=1$, $p=0.063$).

Nurse plants had no significant effect on survival across the elevational gradient.

Seedling growth was highest under blackbrush nurse plants at high elevation only (Figure 11; repeated measures ANOVA: height: $F=10.713$, $df=1$, $p=0.005$; leaves: $F=6.429$, $df=1$, $p=0.022$).

To fully understand the nature of these nurse plant effects, cage*nurse plant interactions must also be considered.

Interactions Between Cage and Nurse Plant Treatments

There were significant interactions between the cage and nurse plant treatments at mid- and high elevation. At mid-elevation, without a cage, there was no nurse plant effect and there is a slight negative effect trend of being close to an adult shrub. With a cage, proximity to creosotebush improved emergence the most, followed by proximity to blackbrush (Figure 12; Likelihood ratio $\chi^2=22.093$, $df=2$, $p<0.001$).

At the highest elevation, cage*nurse plant interactions on cumulative emergence were also significant (Likelihood ratio $\chi^2=5.489$, $df=1$, $p=0.019$), but this interaction was of an entirely different nature. Here, there was no nurse plant effect under cages, and uncaged seedlings emerged with higher rates in open plots (Figure 13).

A similar interaction occurred with survival at mid-elevation. Cage effects were not significant for seedlings in the open but only in combination with creosotebush and blackbrush nurse plants (Figure 15; Log-rank test: in the open: $\chi^2=0.096$, $p=0.756$; creosotebush: $\chi^2=66.343$, $p<0.001$; blackbrush: $\chi^2=6.082$, $p=0.014$). Without a cage, seedlings had higher survival under blackbrush than under creosotebush (Figure 14).

Maximization of Density

Here I consider what treatment combinations maximized density at the three sites. Seedling density was low, ranging from about 13 seedlings (8.6%) to 18 seedlings (11.8%) of all sown seeds per plot on the date of maximal density, but it differed by site (Figure 15). On the last census date, the average seedling density per plot increased with increasing elevation (Likelihood ratio $\chi^2=50.331$, $df=2$, $p<0.001$).

Across the elevational gradient, the caged plots generally had the highest average seedling densities per plot on the last census date (Figure 16). Therefore, considering the

seeds that were planted under “natural conditions” (without use of a cage or seed balls), average seedling density was highest at low elevation and lowest at high elevation. At low and mid-elevation, the caged plots near creosotebush resulted in the highest seedling density per plot on the last census date (Figure 16a and b). Creosotebush had the opposite effect on density in uncaged plots at mid-elevation (Figure 16b). The blackbrush nurse plant had no effect on seedling density at high elevation (Figure 16c).

Experiment 2

At low and high elevation, emergence from bare seeds was higher than for either seed ball recipe (Site 1: Likelihood ratio $\chi^2=63.367$, $df=2$, $p<0.001$; Site 3: Likelihood ratio $\chi^2=12.697$, $df=2$, $p=0.002$). At mid-elevation, all seed treatments resulted in statistically equal emergence rates (Likelihood ratio $\chi^2=1.989$, $df=2$, $p=0.370$). At all sites, mean emergence from both seed ball recipes was less than one seedling per plot, which was true for seed ball emergence in year 1 of Experiment 1 as well. However, in Experiment 2, emergence from bare seed was also lower than in the first year of experiment 1; an average of 5 seedlings per plot compared to 26 seedlings per plot in the first experiment.

Of all seedlings that emerged from seed balls, 0.4% emerged from recipe 1 and another 0.4% from recipe 2. This is far less than the 3.2% of all seedlings that emerged from bare seed in this experiment. For comparison, those percentages in the first growing season of Experiment 1 for the no cage, no nurse plant experimental groups were 0.1% for seed balls and 13.7% for bare seeds. Thus, in the first growing season of the first experiment, for every one seedling that emerged from seed balls, 82 seedlings emerged

from bare seeds, while in the second experiment the ratio was 1:8 seedlings for each recipe. Even though emergence from bare seeds was much lower in the second experiment relative to the first, emergence from seed balls was comparatively higher, suggesting that the new seed ball recipes resulted in higher emergence. Precipitation was likely sufficient for germination as an average of 98.5 mm of rain or snow was recorded at the rain gauges between the planting date and first census date.

Discussion

Precipitation, Soil Moisture, and Soil Temperature

Both years of the study were unusually wet due to an El Niño phase of the ENSO cycle, which typically brings wet winters to the southwestern US (Hereford et al. 2004). I was therefore fortunate to observe as much seed germination as I did, and the study period may well be representative of the rare conditions that can result in an establishment event for blackbrush. A fall rainfall of at least 25 mm in the Mojave Desert is needed to stimulate vegetative and reproductive growth of most shrubs (Beatley 1974). Under conditions of extraordinarily early spring rains (unpredictable in this region), blackbrush seeds germinate in relatively large numbers and these may be the only conditions under which significant recruitment occurs for this species (Beatley 1974). All sites received nearly identical precipitation amounts, which was unexpected since precipitation usually increases with elevation (Ostler and Hansen 2001, Rowlands 1995). The main climatic difference between sites was therefore temperature. The cooler temperature at higher elevation kept the soil at 10 and 30 cm depth wetter for longer.

While this favored eventual seedling growth and survival, the cooler temperature also delayed emergence.

Seed Ball Effects (Hypothesis 1)

My hypothesis that seed balls would have the strongest positive effect at mid-elevation was not supported, at least over the elevational range tested. In fact, seed balls inhibited and delayed emergence across all elevations, thereby decreasing the amount of time a seedling was able to use soil water. Consequently, seed balls had negative effects on growth at the drier sites. Seedling height and number of leaves were not suppressed by seed balls at high elevation, perhaps because water availability was less constraining to growth or emergence was not as delayed as at low elevation.

Seed balls have traditionally been used in more mesic, particularly agricultural, environments (Caplan et al. 1999) and a quantitative evaluation of their efficacy for more arid environments has been lacking. My study suggests that seed balls in arid environments may not aid germination per se, but rather enable seed survivorship from year to year. The thick layer of clay surrounding the seed may have the opposite effect from what is anticipated; rather than extending moisture exposure of the seed coat, it may shorten exposure time by delaying water infiltration. Thus, seed balls may have a function equivalent to dormancy, which prevents a germination response to rain.

Theoretically, a manager may be able to fine tune the “degree of dormancy”, i.e. percent germination or the amount of rain necessary to induce germination by altering seed ball thickness, as it would take longer for water to infiltrate through a thicker layer of clay mixture surrounding the seed. The difference in the emergence from seed balls in

experiment 1, where larger, rounder balls were used, and in experiment 2, where smaller, flatter balls with less clay content were used, supports this hypothesis. Both in terms of the percent of emergence from seeds sown as seed balls (0.1% vs. 0.4%), as well as in relation to the emergence rate observed for bare seeds (1:82 vs. 1:8), the smaller, flatter seed balls produced more seedlings in the first year after sowing. We cannot assume, however, that environmental conditions were equally conducive to germination. For example, precipitation between planting and first emergence was about 40 mm and 100 mm in experiments 1 and 2, respectively. However, using emergence from bare seeds as a measure of environmental suitability (or seed quality), emergence was more than 4 times higher in experiment 1. While my conclusion cannot be conclusive at this stage, experimental results so far suggest that seed ball recipe, shape and size could be a very effective tool for manipulating the degree of germination inhibition.

The evidence that enclosure in seed balls facilitated survivorship was seen in the much higher number of seedlings that emerged from seed balls compared to bare seed in the second year of Experiment 1. In addition, the longer exposure to the elements may have allowed the seed ball casing to loosen and break up more readily, permitting more contact between the seed and moisture and making it easier for seedlings to emerge.

While this result was not what I expected, it opens opportunities to rethink the functionality of seed balls in arid environments. The technique may allow the simulation of a seed bank for species that do not naturally have them. In blackbrush, seeds have dormancy and can germinate even after fifteen years in storage (Pendleton 2005), but the vast majority of seeds in the seed bank are consumed within a year (Meyer and Pendleton 2005).

The existence of a persistent seed bank is a common life history strategy in desert annuals (Adondakis and Venable 2004, Clauss and Venable 2000, Evans et al. 2007, Pake and Venable 1996, Venable 2007, Venable and Lawlor 1980). It is considered a bet hedging strategy, crucial for the persistence of short-lived species that rarely achieve high reproductive output (Pake and Venable 1996, Venable 2007, Venable and Lawlor 1980). Seed banks are not as important for long-lived perennials since the adults live long enough to eventually recruit. However, the premature destruction of an entire shrub stand may provide an ecological context for which the introduction of an artificial seed bank for a long-lived species may be sensible. Seed balls may allow seeds to survive for several years and produce seedlings only in high rainfall years. This should increase the probability that some seedlings are able to take advantage of the rare combination of year types that would allow them to pass into a more drought tolerant size class. By contrast, even though broadcasting of bare seed would initially result in larger seedling populations, there is a high probability that all of the seedlings die in the first few years of their existence. In a highly variable and uncertain environment, all species require a persistent life history stage, either as seed or long-lived adult, to be able to take advantage of the rare conditions that permit recruitment. After fire, this stage is critically impaired for blackbrush, and an artificial seed bank could provide an important gap-filling measure until the first persistent adults are re-established.

Cage Effects (Hypothesis 2)

In accordance with my hypothesis, cages had a positive effect on seedling emergence, survival, and density at all sites, and the effect increased with elevation. This

supported my expectation that rodents, rather than insects, reduce the abundance of blackbrush seeds and seedlings, and that predation pressure from rodents would be higher at higher elevation.

Cages also improved seedling growth at mid- and high elevations, and the reason for this is less obvious. The cages could have created a more favorable micro-environment for growth through partial shading, similar to a nurse plant effect. However, this does not explain why this effect of cage was absent at low elevation, where the nurse plant effect was most pronounced. I think it more likely that predators selectively foraged for larger seedlings (Hulme 1994), leaving smaller seedlings that typically had no to few green leaves behind in the uncaged treatment. Seedlings at low elevation were uniformly smaller, which could have eliminated a noticeable size selection effect.

It is clear that predator exclusion cages contribute strongly to seedling survival and density, especially so at the higher elevations inside the core of the blackbrush community. If it is true that rodents prefer larger seedlings, then they select against the individuals that have the best chance of surviving the harsh environment. However, exclusion cages are costly to implement and may not represent a viable strategy for rehabilitating large, burned areas. Nevertheless, it was positive to see that even without cages, some seedlings do escape predation, suggesting that simply increasing the number of seedlings would increase the number of surviving seedlings.

In addition, I observed strong interactions between the cage treatment and the nurse plant treatment, which suggest that predation pressure can be modified by location with respect to adult shrubs.

Nurse Plant Effects (Hypothesis 3)

Proximity to mature plants had mixed effects on emergence, survivorship and growth, due to two opposing forces, a favorable effect through micro-climate and perhaps soil nutrient levels under shrubs, which was seen in the presence of predator exclusion cages, and a negative effect through higher predation near shrubs that became visible through the comparison of caged and uncaged treatments.

Nurse plants increase soil moisture beneath their canopies and facilitative effects are greater in hotter and drier climates (Holmgren et al. 1997). In addition, nutrient availability is higher beneath adult shrubs, and beneath blackbrush in particular (Brittingham and Walker 2000, Housman et al. 2007, Walker et al. 2001), which could explain the higher seedling growth achieved at high elevation. However, rodents and jackrabbits frequently prefer to forage under shrub canopies which reduce the risk of being detected and/or attacked by predators (Longland 1991) and/or have a larger abundance of seeds relative to the intershrub spaces (Reichman and Price 1993).

As expected, with predator exclusion, the nurse plant effect was positive at the lower elevations and neutral at high elevation. Creosotebush had stronger positive effects on emergence relative to blackbrush at mid-elevation, perhaps because it is a taller shrub, which casts a larger shadow and may create wider islands of fertility (De Soyza et al. 1997, Whitford et al. 1997).

At low elevation, nurse plants had positive effects regardless of cage treatment. However, since most sites needing restoration are left with little living vegetation, careful attention to seed placement may not be a generally good investment of limited funds. At mid-elevation, predation negated the nurse plant effect entirely, whereas at high-

elevation, the effect of nurse plants became negative and seedlings actually achieved higher densities in the open. Therefore, generally planting seeds in open gaps would be better for restoration success.

Synthesis

Blackbrush seeds must pass through several environmental filters for successful establishment. First, seeds must be in the ground at the right time (with imminent cool, wet weather) and escape predation. Second, the winter and early spring must be wet enough for seeds to germination. Third, to escape the harsh summer conditions and more predation pressure, seedlings must grow to a critical size by early spring. Two wet years in a row may ultimately be required to attain a size that endows recruits with the necessary degree of environmental resilience (Goldberg and Turner 1986, Meyer and Pendleton 2005). However, in wet years, rodent abundance is typically also higher (Jensen 1982, Taitt 1981), which increases predation risks unless there are sufficient alternative food sources for rodents or food availability exceeds demand so that some seeds and seedlings can escape predation. Rodent populations peak with some delay behind the peak of food availability, which may give seedlings a better chance of survival in the first of two wet years.

Considering the entire life history context of blackbrush, the long-term success of its restoration may depend on a very specific constellation of circumstances (e.g. two high precipitation years, low predation pressure) that are largely out of management control. Thus, achieving high germination rates in any arbitrary year may have zero long-term success. This suggests that a strategy which works with natural environmental

cycles, and a more subtle manipulation of ecological and environmental odds, may have a greater chance of success.

Perhaps the most important conclusion from our study is that the ostensibly negative effect of encapsulating seeds in seed balls may have a long-term benefit by enabling blackbrush to have a persistent seed bank and thus being better able to hedge bets on year types. Even in thriving blackbrush populations, recruitment opportunities are limited by seed masting dynamics (Meyer and Pendleton 2005). For example, if a seed masting year is not followed by suitable precipitation patterns, despite of the elevated reproductive effort, no recruitment may result. Conversely, if the constellation of favorable conditions occurs, but seed availability happens to be low, very little recruitment may occur. By the same token, if the broadcasting of seeds in a burnt area is not followed by sufficient precipitation, or if predator densities happen to be high, restoration efforts are negated. However, if restoration focuses on having viable seeds in the ground at any time, the favorable constellation of conditions will meet with some success every time. Future follow-up observations of my experimental plots will provide opportunities to further test this hypothesis.

The information gleaned from this experiment not only permits the development of restoration techniques, it also provides insights into potential effects of climate change on the blackbrush community to indicate where today's restoration efforts should be focused. It appears that over the course of two growing seasons with favorable precipitation, climate differences between elevations (mainly soil moisture due to temperature differences) affected blackbrush seedling survival and growth. With a hotter and drier climate expected at the lower elevational and latitudinal range limits of this

species, restoration efforts may have more long-term success at higher elevations within the Mojave Desert and should be the primary focus. Anticipated impacts from climate change are also likely to increase the variability of having two consecutive favorably wet years, presenting yet another challenge to restoration success. Therefore, it is of even more importance that these rare windows of opportunity for restoration be exploited by already having seeds in the ground to take advantage of rare years. El Niño forecasts are currently being used for reforestation projects in Peru (Holmgren et al. 2006) and climate considerations should be used to reduce the risk of unsuccessful recruitment in arid environments. However, while recruitment success would likely be higher during wet periods, effects may be jeopardized by increased fire frequency in dry years (Holmgren et al. 2006). Management of fire regimes will be paramount to conserving blackbrush communities, as frequent fires not only threaten restoration projects, but also promote exotic annual grasses. Wildfire season severity can be predicted up to a year in advance (Westerling et al. 2003), providing another useful tool to predict the occurrence of conditions that is conducive to successful recruitment. Wetter sites therefore are likely the best option not only because of the demonstrated higher seedling success rate there, but higher soil moisture indicates areas less prone to fire (Westerling et al. 2003) and exotic grass invasion (Condon et al. 2011).

This approach to restoration by analyzing specific vulnerabilities and their influences on plant recruitment, as well as considering the plant's life history strategies and using methods to overcome their natural limitations, can be used as a model for other threatened plant communities in a variety of contexts. Adaptive management is

particularly relevant considering predicted future climatic changes and human impacts to natural environments.

Table 1. Site locations and experimental design.

	Low Elevation	Mid-Elevation	High Elevation
Elevation	1,260 m	1,305 m	1,510 m
Geographic coordinates	35°28'25.87" N 115°38'12.95" W	35°28'41.41" N 115°37'42.58" W	35°28'25.76" N 115°35'31.89" W
Soil depth	> 1 m	65 cm	30 cm
Vegetation community	Creosotebush dominant with a variety of cacti and yucca species.	About equal abundance of blackbrush and creosotebush. Also a variety of cacti and yucca species.	Blackbrush dominant with yucca species.
Seeds per plot	150	150	150
Number of plots	24	36	24
Factor 1: Seed application	Seed ball/direct seeding	Seed ball/ direct seeding	Seed ball/ direct seeding
Factor 2: Exclusion cage	Cage/no cage	Cage/no cage	Cage/no cage
Factor 3: Nurse plant	Open/N-side of creosotebush	Open/N-side of blackbrush/N-side of creosotebush	Open/N-side of blackbrush
Factor replicates	3	3	3

Table 2. Density of the dominant perennial shrub and stem succulent species at the 3 study sites.

Dominant Shrubs	Low Elevation	Mid-Elevation	High Elevation
Total density per m²	2.22	1.78	4.66
Species richness	16	12	15
<i>Coleogyne ramosissima</i>	0.90%	1.12%	64.38%
<i>Ephedra nevadensis</i>	23.42%	30.34%	Included in “other”
<i>Hymenoclea salsola</i>	18.92%	Not found	Included in “other”
<i>Krameria erecta</i>	12.61%	16.85%	Not found
<i>Larrea tridentata</i>	10.81%	8.99%	0%
<i>Thamnosma montana</i>	Included in “other”	Not found	8.15%
<i>Yucca baccata</i>	Included in “other”	Included in “other”	6.01%
<i>Yucca schidigera</i>	Included in “other”	13.48%	7.30%
Other shrubs	33.33 %	39.33%	14.16%

Table 3. Percent cover of dominant perennial shrub and stem succulent species at the 3 study sites.

Dominant Perennials	Low Elevation	Mid-Elevation	High Elevation
Total plant cover	21.31%	20.02%	30.33%
<i>Coleogyne ramosissima</i>	0.08%	0.29%	20.12%
<i>Ephedra nevadensis</i>	Included in “other”	4.12%	Included in “other”
<i>Larrea tridentata</i>	6.36%	1.65%	0%
<i>Lycium andersonii</i>	2.40%	Not found	Not found
<i>Opuntia acanthocarpa</i>	2.45%	2.08%	Included in “other”
<i>Thamnosma montana</i>	Not found	Not found	1.34%
<i>Yucca baccata</i>	Included in “other”	Included in “other”	3.54%
<i>Yucca schidigera</i>	2.78%	4.22%	3.75%
Other plants	7.26%	7.68%	1.59%

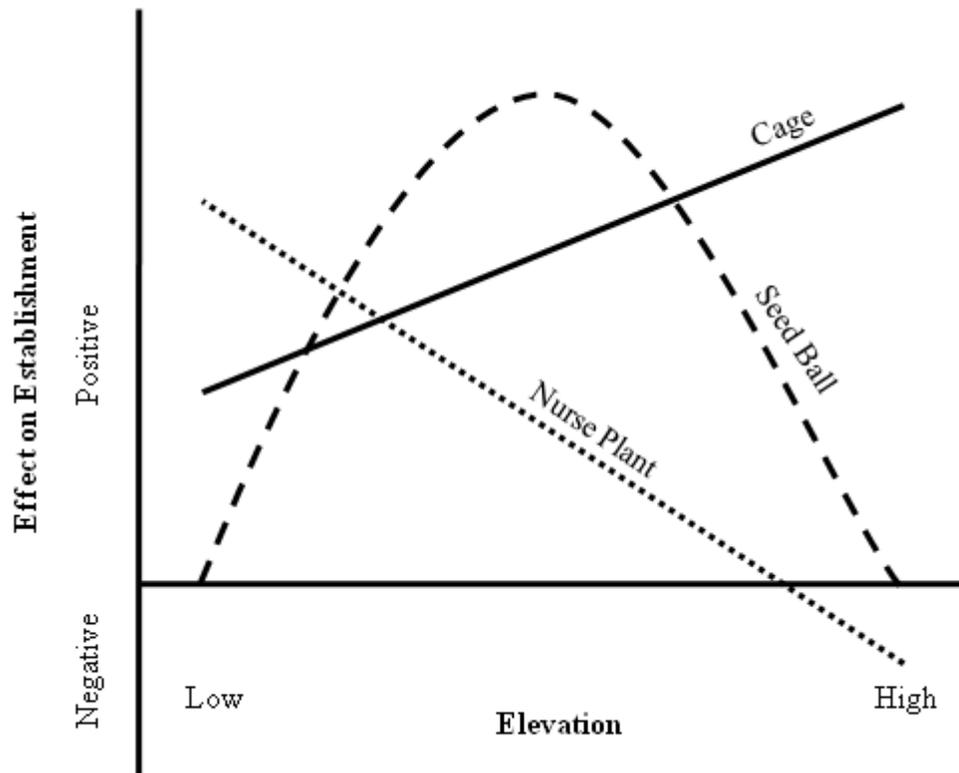


Figure 1. Expected effects of restoration methods on establishment as a function of elevation.



Figure 2. Google Earth satellite photograph of the 3 study sites in Mountain Pass, CA. Site 1 is low elevation, Site 2 is mid-elevation, and Site 3 is high elevation, with a 250 m elevational difference between the low and high elevation sites.

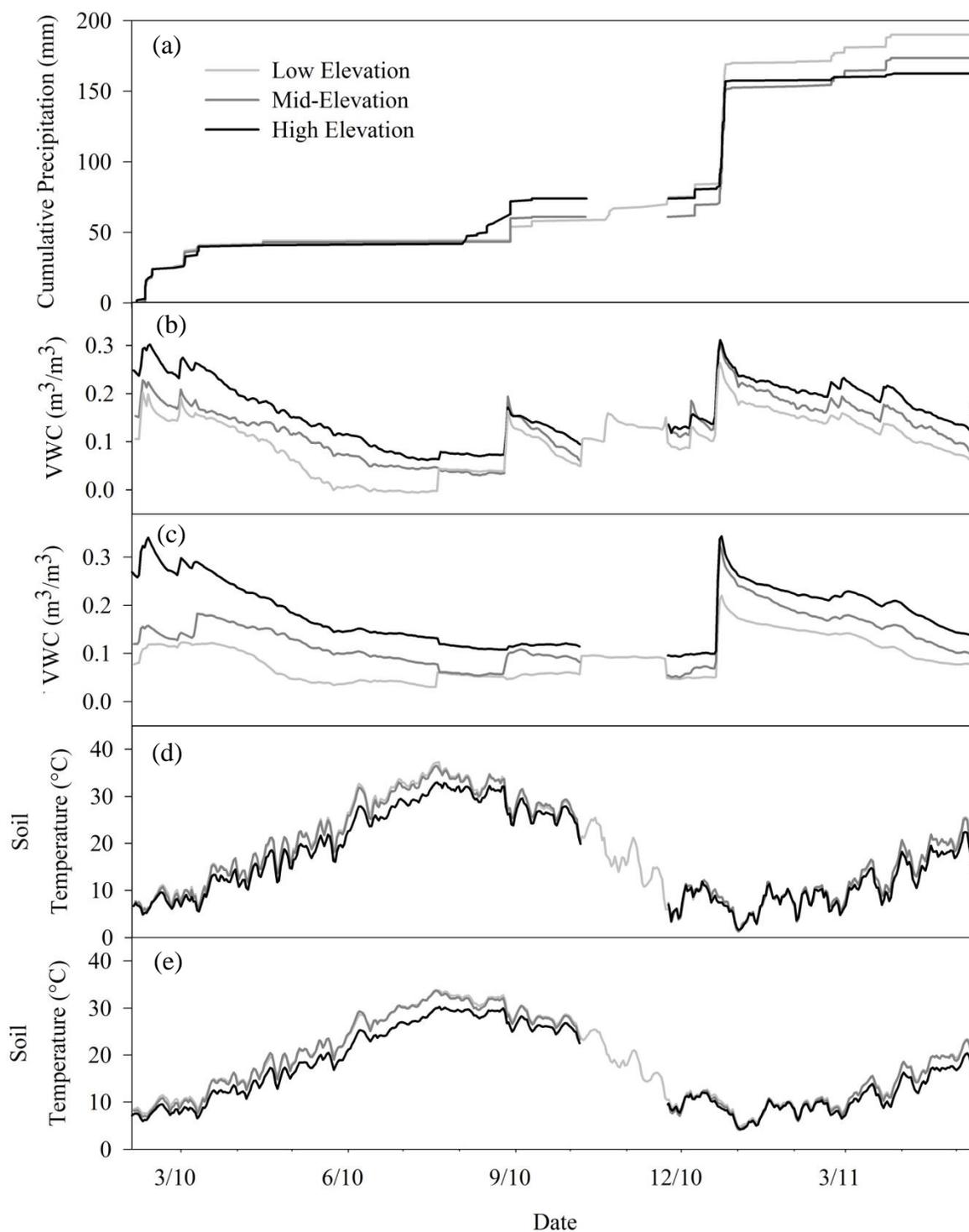


Figure 3. Cumulative precipitation (a), average volumetric soil water content at 10 cm (b), and 30 cm (c) depth, and average soil temperature at 10 cm (d) and 30 cm (e) depth at the 3 study sites. A second replicate of all probes was added to each site on July 20, 2010. Data loss for mid- and high elevation sites occurred from October 7th to November 22nd, 2010.

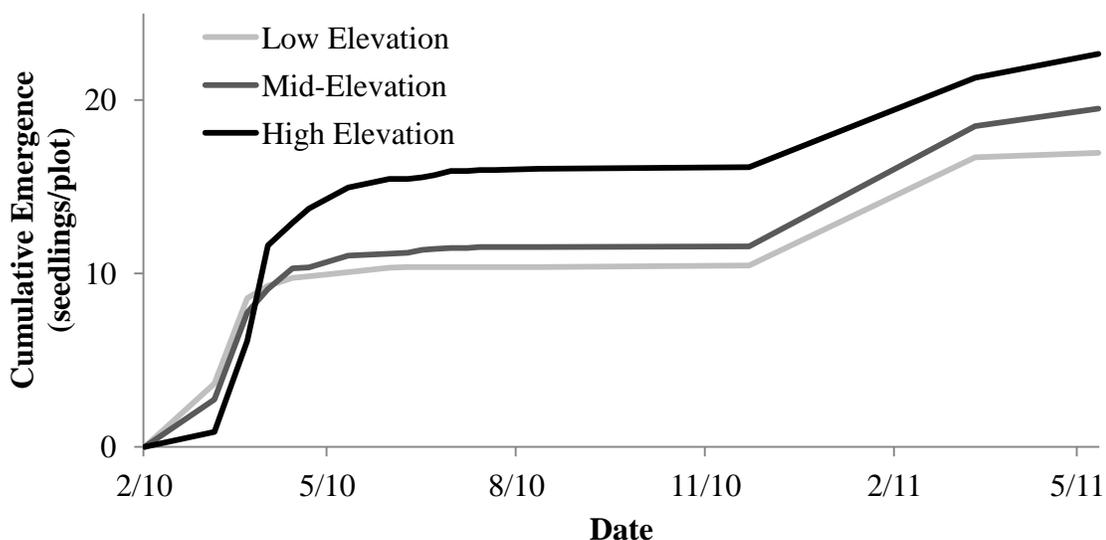


Figure 4. Cumulative seedling emergence per plot over time by site. Cumulative emergence was highest at the high elevation site for most of the study though on the last census date there is no significant difference between sites.

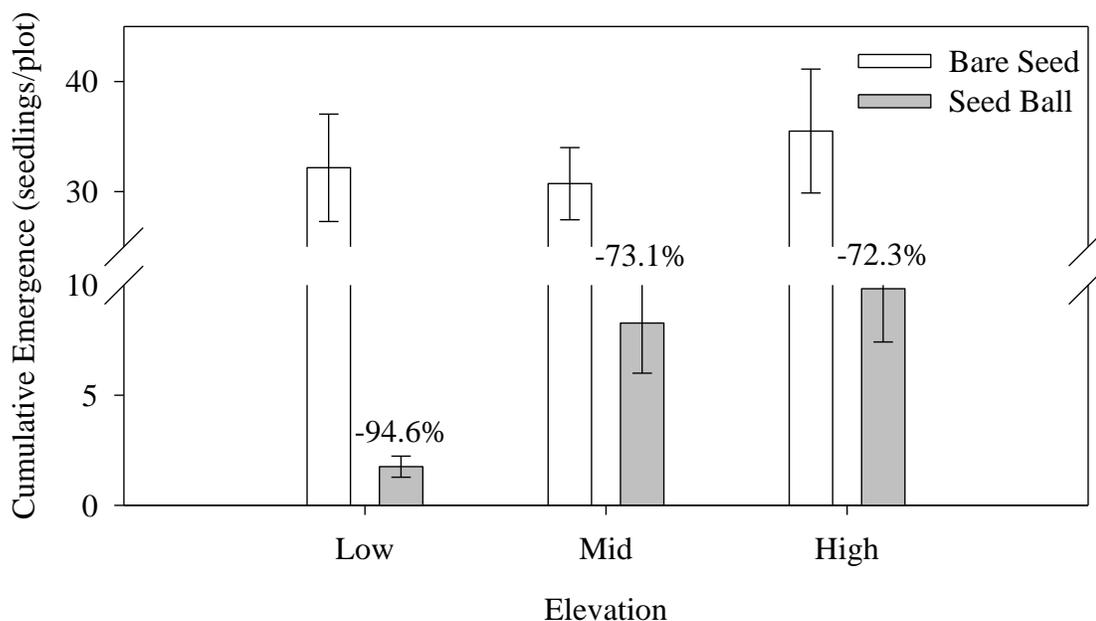


Figure 5. Cumulative seedling emergence per plot for seeding treatment. Mean number of seedlings per plot with standard error bars and percent loss from seed balls relative to bare seed are shown. Emergence from bare seed was significantly higher than emergence from seed balls at all sites.

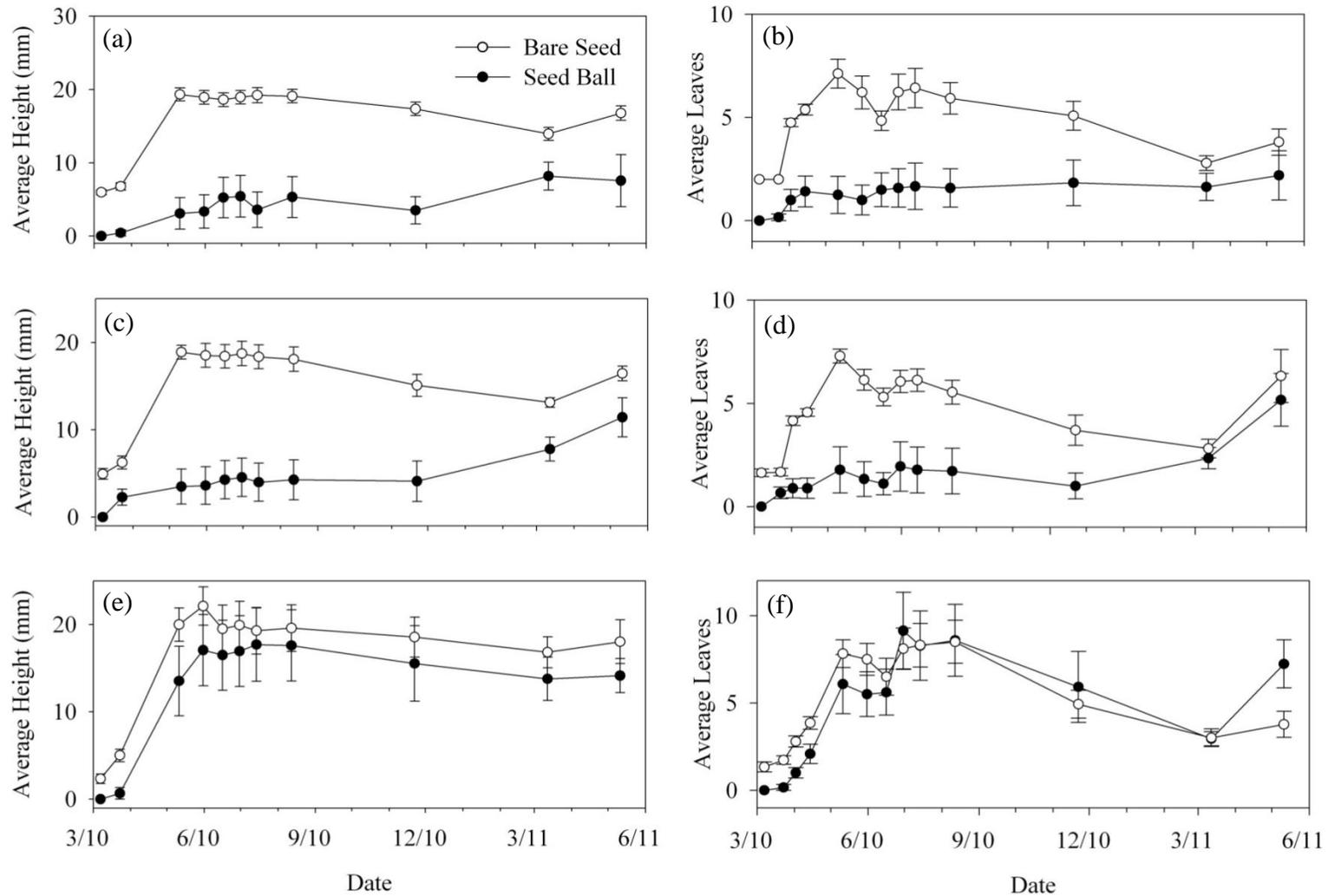


Figure 6. Average seedling height and number of leaves at low (a, b), mid- (c, d), and high (e, f) elevation by seeding treatment. Mean values with standard error bars shown. Growth was better with the bare seed treatment at low and mid-elevation only.

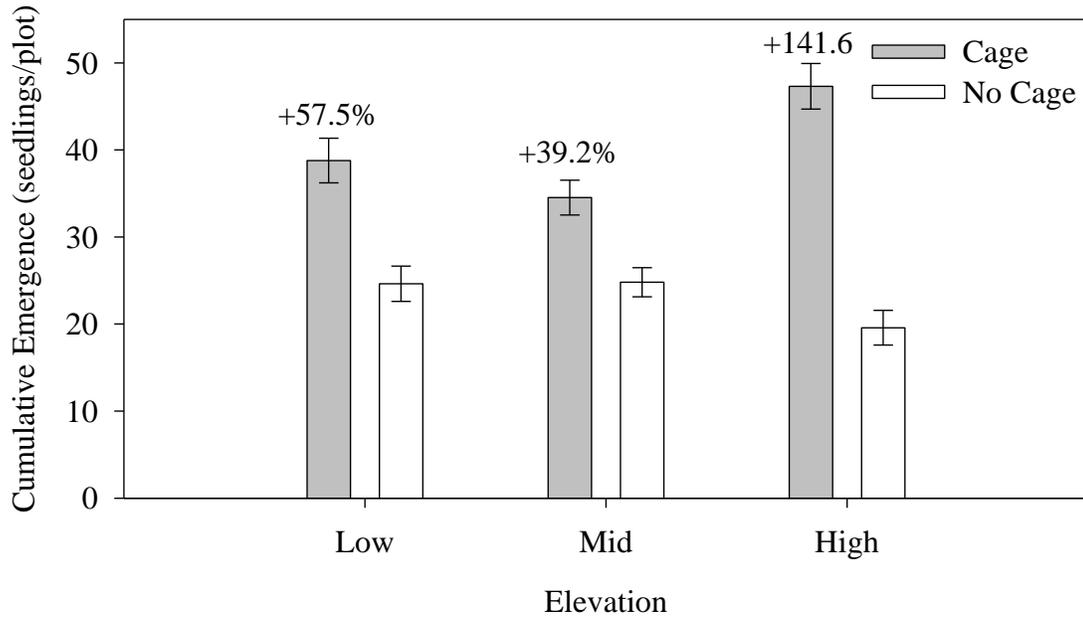


Figure 7. Cumulative seedling emergence per plot for cage treatment. Mean number of seedlings per plot with standard error bars and are percent gain from cages relative to no cages shown. Emergence from caged plot was significantly higher than emergence from uncaged plots at all sites.

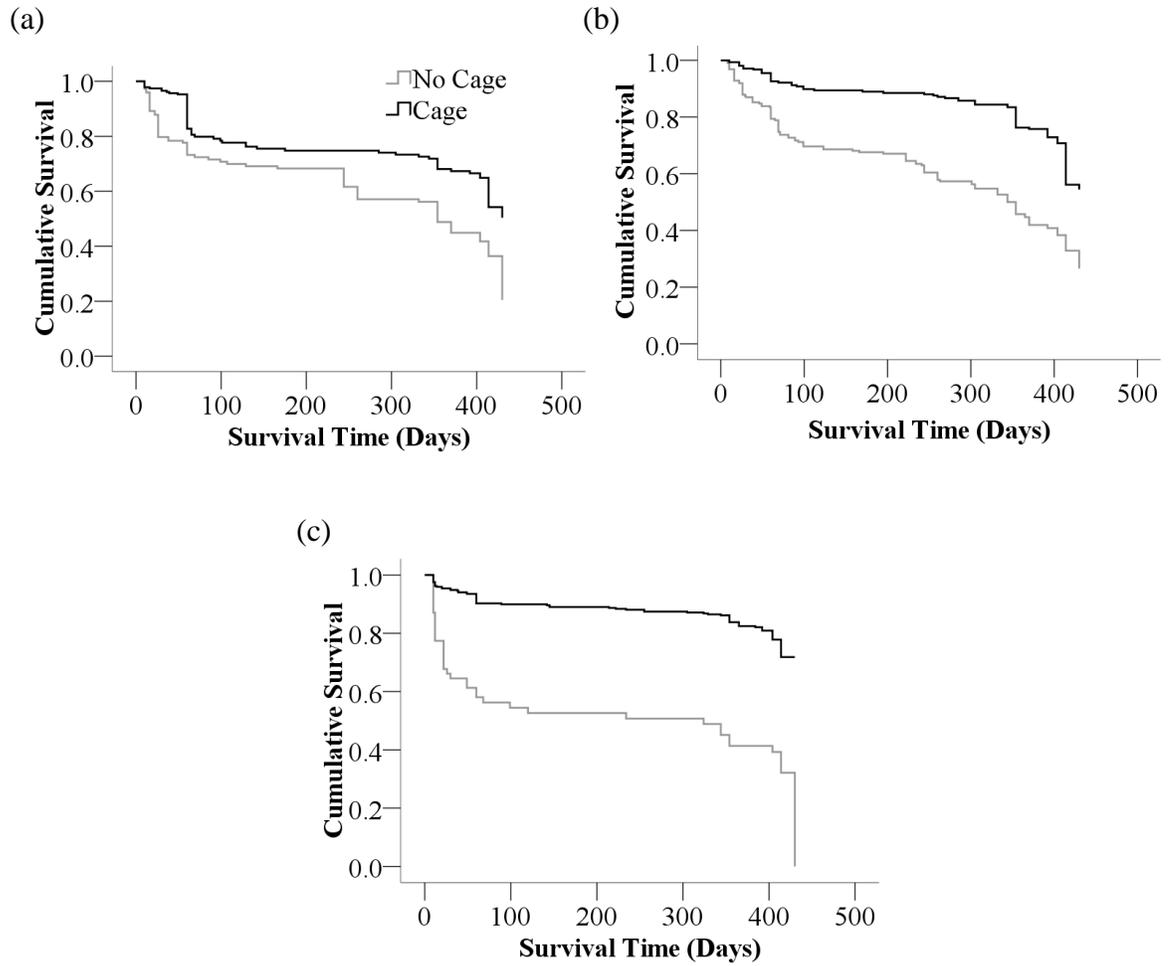


Figure 8. Kaplan-Meier seedling survival curves at low (a), mid- (b), and high elevation (c) for cage effect. Cages significantly increased survival at all sites.

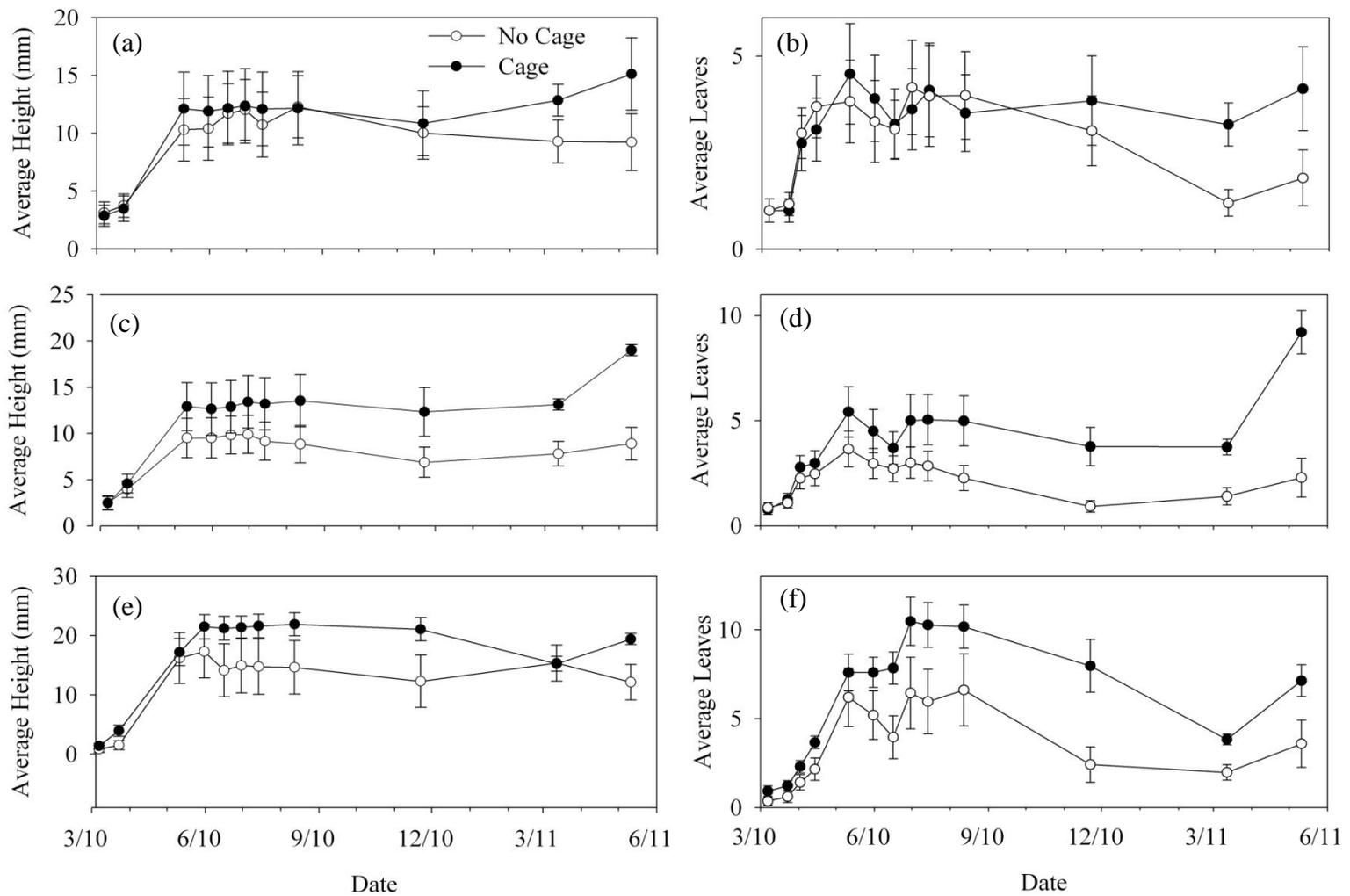


Figure 9. Average seedling height and number of leaves at low (a, b), mid- (c, d), and high (e, f) elevation by cage treatment. Mean values with standard error bars shown. Growth was better for caged seedlings at mid- and high elevation only.

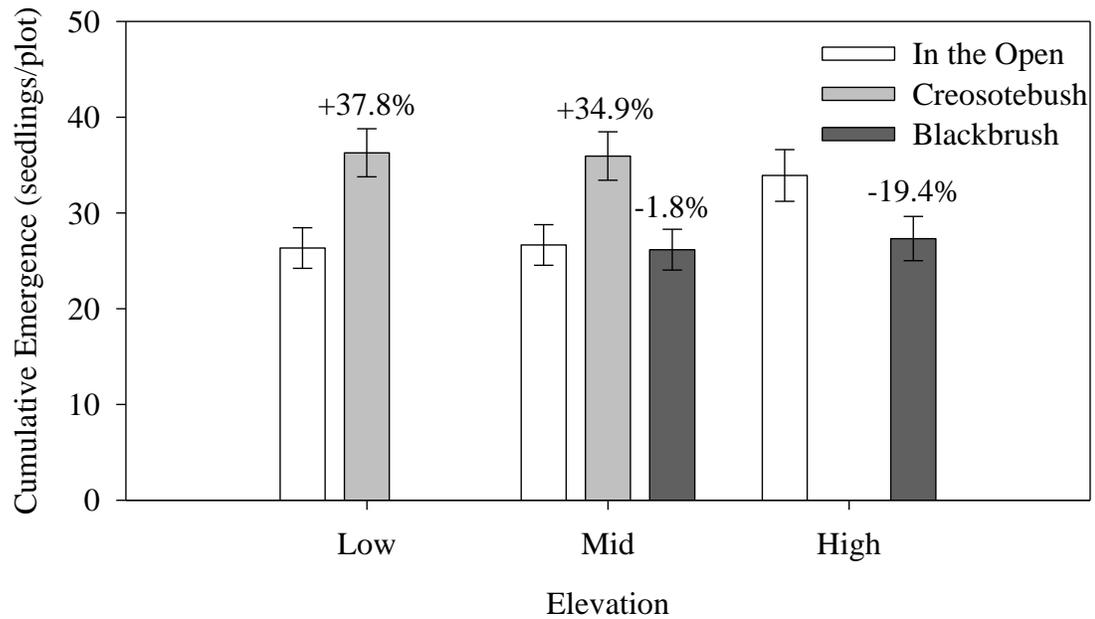


Figure 10. Cumulative seedling emergence per plot for nurse plant treatment. Mean number of seedlings per plot with standard error bars and percent gain or loss relative to plots in the open shown. Seedling emergence was significantly higher with creosotebush nurse plants at low and mid-elevation.

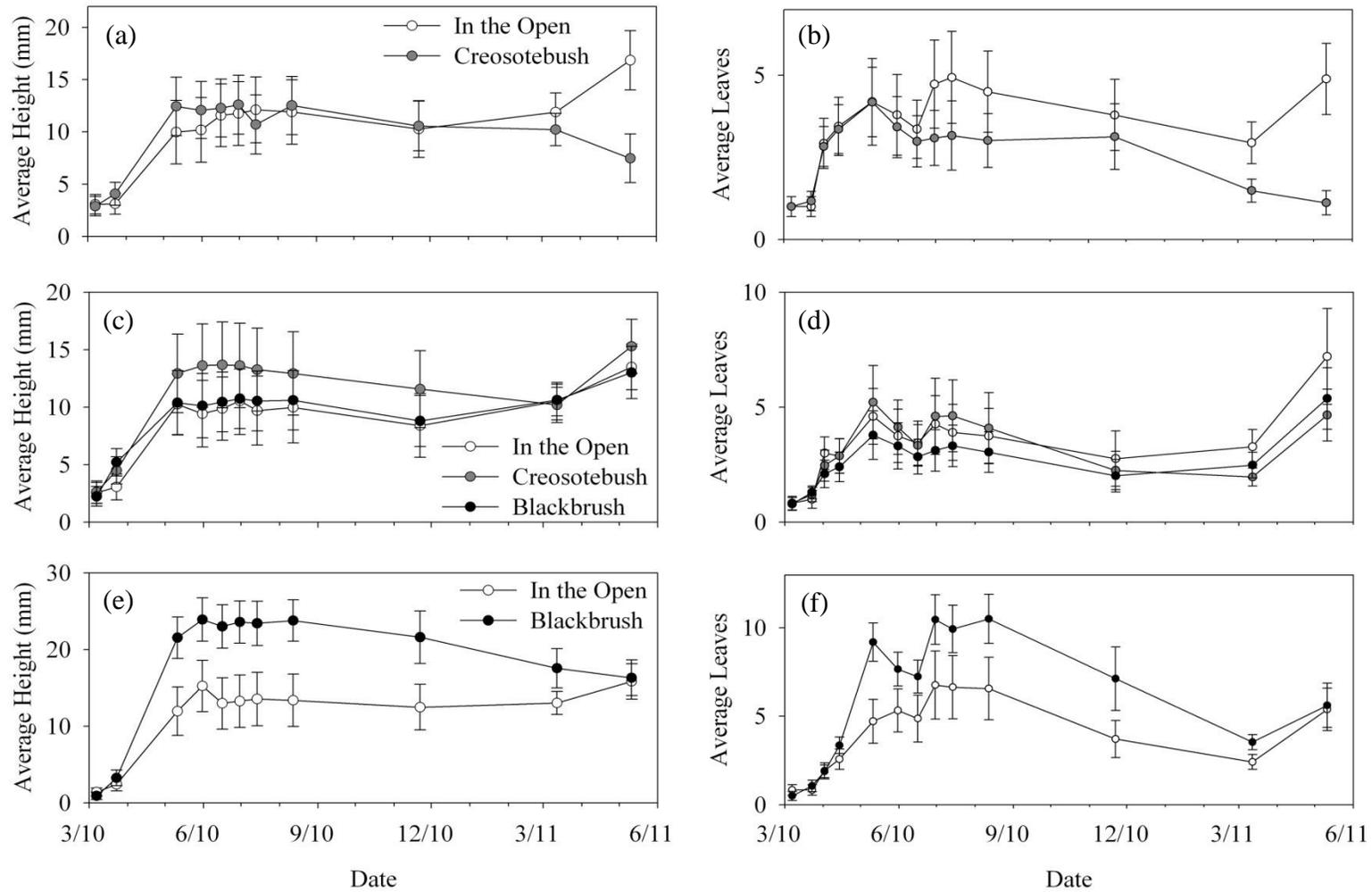


Figure 11. Average seedling height and number of leaves at low (a, b), mid- (c, d), and high (e, f) elevation by nurse plant treatment. Mean values with standard error bars shown. Growth was better for seedlings near blackbrush nurse plants at high elevation only.

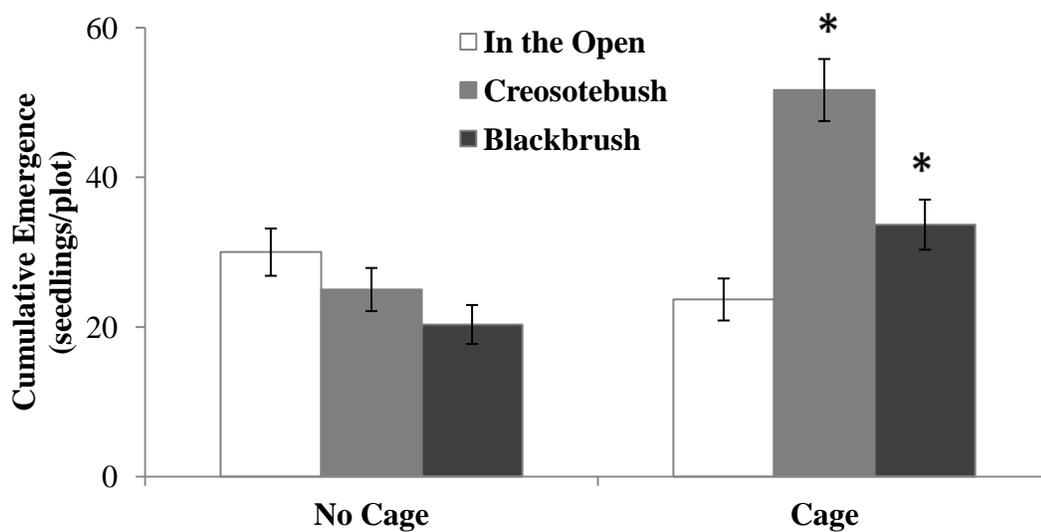


Figure 12. Cage*Nurse plant interaction at mid-elevation. Mean number of seedlings per plot with standard error bars are shown. Asterisks (*) indicate significant effects of nurse plant on seedling numbers within the cage treatment.

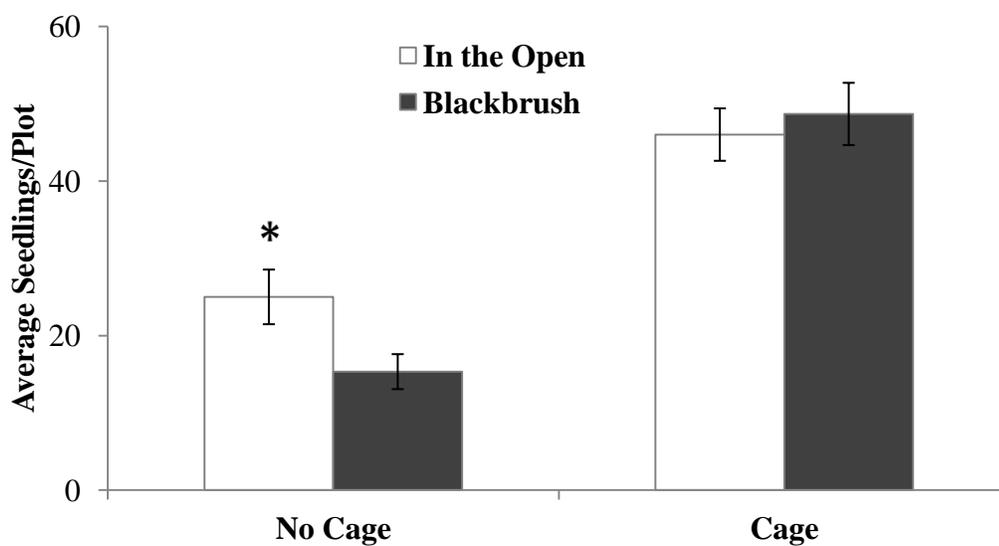


Figure 13. Cage*Nurse plant interaction at high elevation. Mean number of seedlings per plot with standard error bars are shown. Asterisk (*) indicates a significant effect of nurse plant on seedling numbers within the cage treatment.

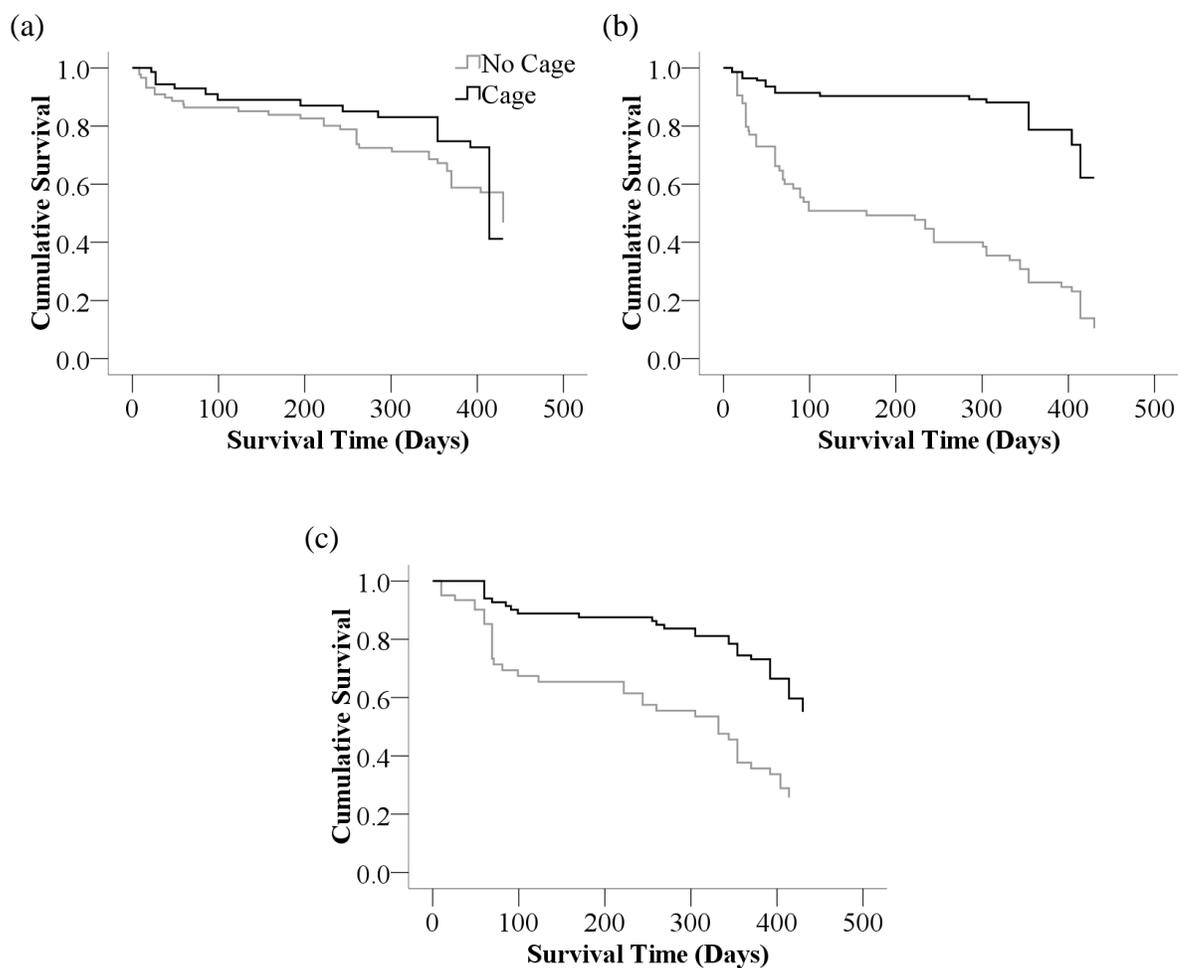


Figure 14. Kaplan-Meier seedling survival curves at mid-elevation for plots in the open (a), under creosotebush (b) and under blackbrush (c). Cages improved survival for seedlings near nurse plants. For seedlings under shrubs without a cage, blackbrush improved survival relative to creosotebush.

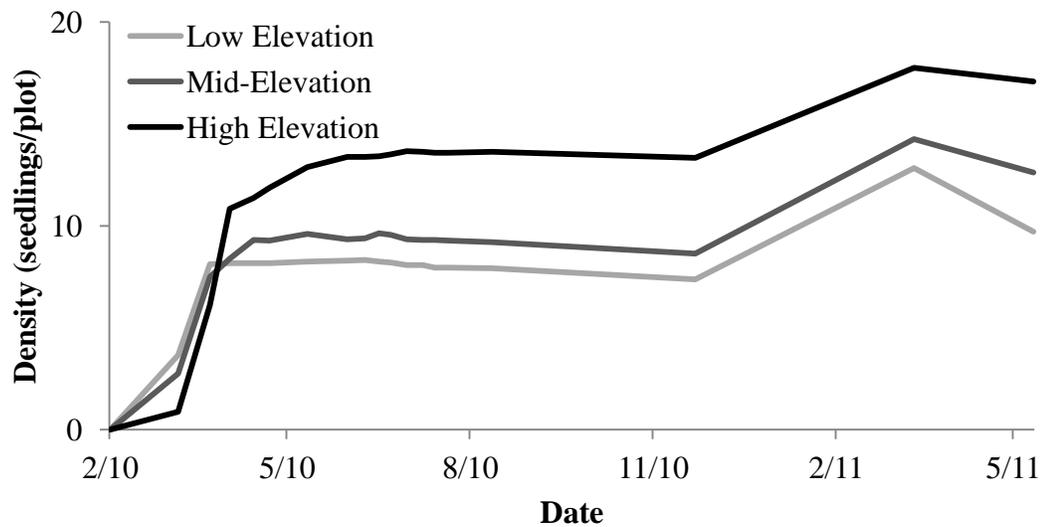


Figure 15. Average seedling density per plot by site. Density was highest at the highest elevation.

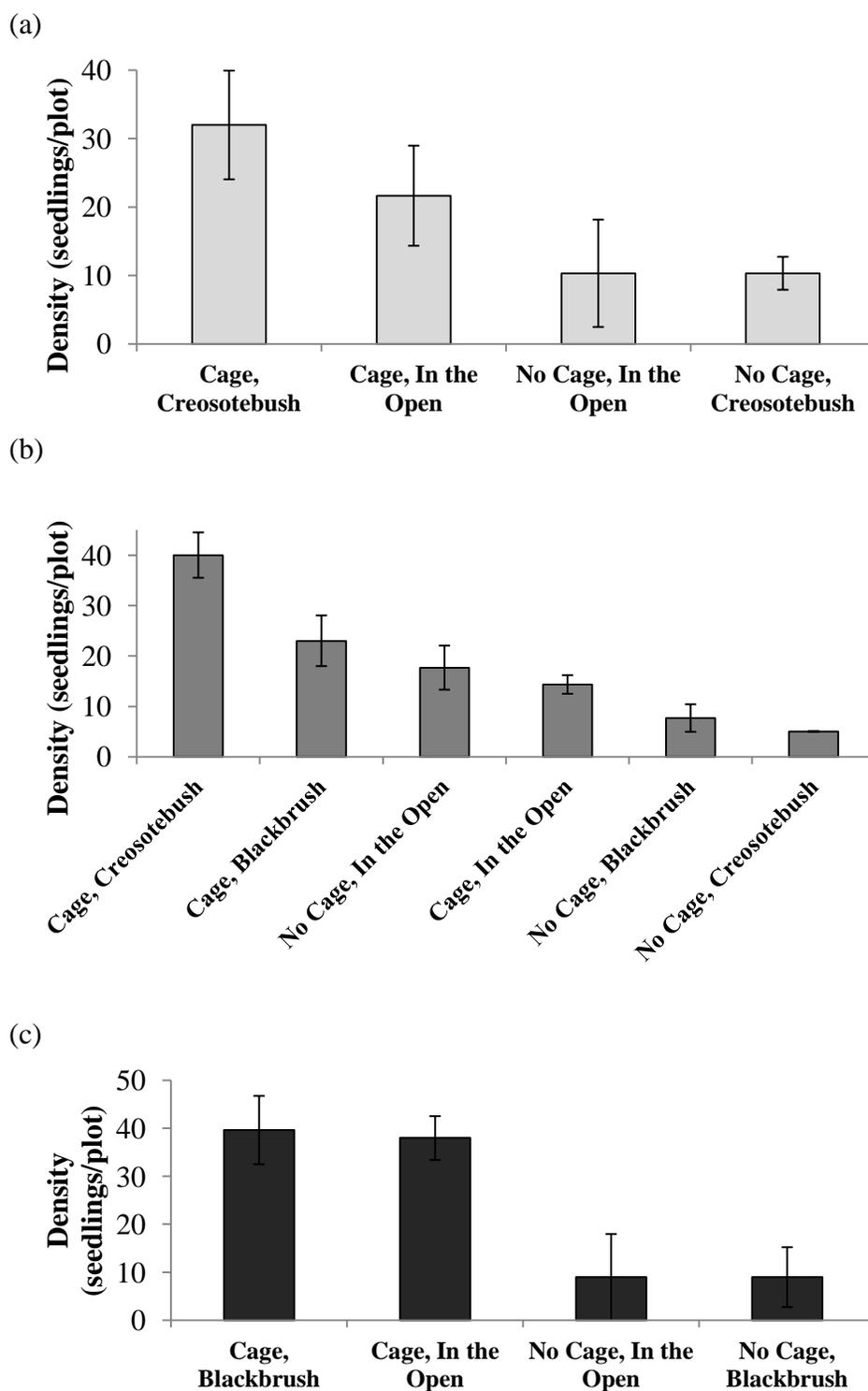


Figure 16. Average seedling density by treatment at low (a), mid- (b), and high (c) elevation. Mean number of seedlings per plot with standard error bars are shown. On the last census date, caged plots at all sites generally had the highest densities. At low and mid-elevations, the cage, creosotebush treatment combination had the highest densities. There was no nurse plant effect at high elevation.

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