



Original article

Seedling establishment in a masting desert shrub parallels the pattern for forest trees

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ABSTRACT

The masting phenomenon along with its accompanying suite of seedling adaptive traits has been well studied in forest trees but has rarely been examined in desert shrubs. Blackbrush (*Coleogyne ramosissima*) is a regionally dominant North American desert shrub whose seeds are produced in mast events and scatter-hoarded by rodents. We followed the fate of seedlings in intact stands vs. small-scale disturbances at four contrasting sites for nine growing seasons following emergence after a mast year. The primary cause of first-year mortality was post-emergence cache excavation and seedling predation, with contrasting impacts at sites with different heteromyid rodent seed predators. Long-term establishment patterns were strongly affected by rodent activity in the weeks following emergence. Survivorship curves generally showed decreased mortality risk with age but differed among sites even after the first year. There were no detectable effects of inter-annual precipitation variability or site climatic differences on survival. Intraspecific competition from conspecific adults had strong impacts on survival and growth, both of which were higher on small-scale disturbances, but similar in openings and under shrub crowns in intact stands. This suggests that adult plants preempted soil resources in the interspaces. Aside from effects on seedling predation, there was little evidence for facilitation or interference beneath adult plant crowns. Plants in intact stands were still small and clearly juvenile after nine years, showing that blackbrush forms cohorts of suppressed plants similar to the seedling banks of closed forests. Seedling banks function in the absence of a persistent seed bank in replacement after adult plant death (gap formation), which is temporally uncoupled from masting and associated recruitment events. This study demonstrates that the seedling establishment syndrome associated with masting has evolved in desert shrublands as well as in forests.

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1. Introduction

Masting, defined as the synchronous intermittent production of large seed crops by perennial plants, is a well-known phenomenon that has been investigated empirically for a wide range of species (Kelly and Sork, 2002) and that has recently received considerable theoretical attention (Tachiki and Iwasa, 2010, 2012; Kelly et al., 2013; Tamburino and Bravo, 2013). A frequently proposed explanation for the evolution of masting is predator satiation (Janzen, 1971; Silvertown, 1980; Kelly, 1994). The production of a large seed crop following inter-mast years with low seed production is thought to permit escape of some fraction of the mast year crop from seed predators, whose numbers have declined during the

inter-mast years and do not respond quickly enough to take full advantage of the resource pulse represented by masting. The seed predators may be pre-dispersal predators that consume seeds, or they may be post-dispersal predators that often carry out secondary dispersal of seeds as well as consuming them. One of the best studied systems is scatter-hoarding, in which the vertebrate predator, usually a rodent or bird, removes seeds from the vicinity of the parent plant and caches them in shallow surface scatter-hoards or caches that may provide an optimum environment for seedling establishment (VanderWall, 2010). In inter-mast years when seed resources are limiting, few or no seeds remain in scatter-hoards to emerge in spring. It is only immediately following mast years that some seeds remain in caches long enough to produce emerged seedlings.

High post-dispersal seed predation may select for seeds that do not form persistent seed banks, yet mast events are rarely tied

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temporally to the disturbance regimes that create openings for new plants in closed communities. For these reasons a common pattern in masting tree species is the formation of ‘seedling banks’ (Grime, 1979). These plants establish after mast events, grow very slowly, and remain in the juvenile condition for extended time periods, largely because their growth is suppressed by competition from conspecific adults. These suppressed plants are poised to resume normal growth when gap formation takes place (Szwagrzyk et al., 2001; Alvarez-Aquino and Williams-Linera, 2002; Cruz-Rodriguez and Lopez-Mata, 2004; Antos et al., 2005). They are often the primary source of new trees following the loss of adult trees in forests, for example, following insect outbreaks (DeRose and Long, 2010; Rossi and Morin, 2011).

Conspicuously lacking in the large body of knowledge on masting is any explicit discussion of mast seeding in deserts. The high inter-annual variability in seed production observed in deserts is usually assumed to be a direct consequence of differences in current-year growing season quality due to variation in the amount and timing of precipitation (Beatley, 1974). By scaling seed production to current-year growing conditions, desert perennials may maximize seed production over time (resource matching; Kelly and Sork, 2002). This reproductive schedule does little to protect seeds from predation, however, because seed predators are presumably tracking the same variation in resource quality as plants.

Seed predators are prominent members of the fauna of desert systems (Brown et al., 1979a). Post-dispersal predation by rodents and ants has been particularly well-studied, though the primary focus of these studies has been seed resource variation due to inter-annual variation in seed production by annual plants (Beatley, 1976; Brown et al., 1979b; Inouye et al., 1980). Annual plant seed production is strongly constrained by current-year growing conditions (Beatley, 1974). In contrast, perennial plants, particularly shrubs, have the potential to produce large seed crops in non-optimal years, if such production increases the fitness of the maternal plant by improving chances of offspring survival. This suggests that mast seeding in desert shrubs could be under positive selection.

The Rosaceous desert shrub *Coleogyne ramosissima* Torr. (blackbrush), a regionally important species along the ecotone between North American warm and cold deserts, exhibits a masting pattern of inter-annual seed production (Pendleton et al., 1995; Pendleton and Meyer, 2004; Auger, 2005). This wind-pollinated species (Pendleton and Pendleton, 1998) forms nearly mono-specific stands over large areas on the shallow, infertile soils where it is the dominant shrub (West, 1983). We took advantage of a mast year (1991) to initiate a series of short and long term studies on the regeneration biology of this little-studied shrub (Pendleton et al., 1995; Pendleton and Pendleton, 1998; Pendleton and Meyer, 2004; Meyer and Pendleton, 2005). These included experimental studies on seed germination and seedling establishment at

climatically contrasting sites in the Mojave Desert (near Hurricane, UT), and on the Colorado Plateau (Salt Valley in Arches National Park, UT; Meyer and Pendleton, 2005). In the spring of 1992, the year following the masting event, we observed emergence of thousands of blackbrush seedlings in clusters from apparent rodent caches at numerous sites across the species range. We followed the fate of the seedlings in these natural caches from emergence through nine growing seasons at four sites chosen to represent a range of climate and soil conditions.

Here we use this nine-year data set to address the hypothesis that establishment patterns exhibited by blackbrush following a mast event are associated with a suite of seed and seedling traits similar to those exhibited by masting species of mesic environments (Tachiki and Iwasa, 2010). We also examine how establishment patterns are mediated through the actions of rodent seed predators that are also agents of dispersal for this species. Specifically, we tested the hypothesis that recruitment, establishment, and growth patterns in blackbrush would result in the formation of ‘seedling banks’, a key component of the masting syndrome in forest species.

2. Materials and methods

We tagged naturally emerging seedlings in spring 1992 at two sites where we had established experimental seeding studies the previous year (Meyer and Pendleton, 2005). These were sandy sites with relatively deep soils, but with contrasting climates (Hurricane and Salt Valley; Table 1). We also tagged naturally emerging seedlings at two additional sites with climates somewhat similar to the original sites, but with shallower, rocky soils (Toquerville and Little Rockies).

Newly emerged blackbrush seedlings were enumerated at each of the four study sites in early to mid-March 1992 by establishing belt transects and tagging and noting the coordinates of all caches observed within each transect. We used numbered aluminum tags on nails flush with the surface to mark the caches, placed approximately 15 cm from the cache in a standard relative position to reduce the possibility of behavioral effects. The transects had a standard width of 5 m but varied in length and total area depending on cache density, so that approximately 400 caches were tagged in intact stands at each site (Table 2). At three of the sites, we also established transects on small-scale disturbances (natural gas pipeline corridors at Salt Valley and Toquerville and an abandoned powerline road at Hurricane). Cache densities were lower on disturbances, resulting in lower numbers of tagged caches (ca. 140–190; Table 2).

At the time of tagging, we counted the number of seedlings in each cache and noted any apparent rodent activity (e.g., excavation). We also noted the position of the cache relative to established

Table 1
Location and site information for four research sites included in the study. Climate data are from: www.prism.oregonstate.edu/.

	Salt Valley	Little Rockies	Hurricane	Toquerville
Latitude	38° 45' 40.65" N	37° 45' 35.54" N	37° 10' 33.30" N	37° 16' 47.82" N
Longitude	109° 36' 02.04" W	110° 39' 06.30" W	113° 20' 18.50" W	113° 18' 41.20" W
Elevation (m)	1497	1700	985	1164
Substrate	Aeolian sand over sandstone	Gravelly alluvium quartz monzonite	Aeolian sand and gravel over basalt	Gravelly alluvium over basalt
Soil Depth (cm)	77	24	74	44
% Surface Rock	<5	60	20	50
% Cryptogamic Crust	30	<10	<5	<5
Slope	10–20%	10–15%	10–15%	5–10%
Aspect	SSW	N	S	SE
Mean Annual Temperature (C)	12.1	12.2	16.7	15.6
Annual Precipitation (mm)	242	230	280	321

Table 2

Emergence census data from blackbrush seedling transects established in spring 1992 in intact stands at four study sites and on pipeline/abandoned road disturbances at three of the sites.

	Salt Valley		Little Rockies	Hurricane		Toquerville	
	Intact stand	Disturbance	Intact stand	Intact stand	Disturbance	Intact stand	Disturbance
Area sampled (m ²)	900	900	300	1200	600	150	600
Caches tagged	442	187	450	380	140	467	152
Seedlings counted	2612	1380	2905	1028	1157	1533	507
Mean seedlings per cache	5.9	7.4	6.5	2.7	8.3	3.3	3.3
Cache density (per m ²)	0.49	0.21	1.5	0.32	0.23	3.1	0.25
Seedling density (per m ²)	2.9	1.5	9.7	0.9	1.9	10.2	3.1

perennial plants using a categorical system (open:>15 cm from the dripline of a perennial plant; adjacent to a blackbrush crown: within 15 cm distance from the dripline; under a blackbrush crown: within the dripline; or adjacent to or under the crown of another perennial species as described for blackbrush). We evaluated the caches a second time approximately six weeks later (late April or early May 1992), noting how many seedlings remained alive in each cache and the apparent cause of death for dead or missing seedlings, as well as noting any new emergence. Mortality causes included death in place (dead plant still present) possibly due to desiccation, obvious excavation, and seedling predation (seedling stem bases present). Many seedlings simply disappeared; the cause of mortality was recorded as unknown. The caches were enumerated again in fall 1992, spring 1993, and spring 1994 using the same protocols. We were unable to continue the study beyond two years at Hurricane because the site was developed for commercial construction. In fall 1994, we enumerated and measured all seedlings in each surviving cache at the remaining sites. We measured individual height and stem caliper for each seedling. The caches were enumerated again in spring 1997 and fall 2000, and maximum height, and in some cases stem caliper and crown diameter, were measured in 2000. We also searched for new seedlings at each census date, but other than a very few seedlings that emerged in 1993, no further blackbrush emergence was observed.

In early summer 1997 we characterized species composition of the nocturnal rodent community at each of the four study sites in two nights of live-trapping with two trap lines of 50 Sherman traps at 5 m spacing. All captured rodents were identified to species and released immediately at the point of capture the following morning. No rabbits were observed at any site during the trapping period; rabbits were only rarely observed during the entire course of the study. White-tailed antelope ground squirrels (*Ammospermophilus leucurus*, a diurnal sciurid) were observed at all sites during the trapping period and on many other occasions.

We obtained 30-year climate data for each site from the PRISM climate database (Table 1). We also obtained monthly weather data for the period October 1992 through September 2000. These data were used to calculate deviations from mean precipitation for each site during periods corresponding to the intervals between seedling census dates.

Count data were analyzed using Poisson regression (SAS Version 9.4 Proc Genmod), a procedure that carries out multiway contingency table analysis. We analyzed count data for both caches and seedlings because establishment of a cache in the open is an event of greater demographic importance than the number of seedlings in that cache, as newly established clumps become foci for additional recruitment over the long term (S. Kitchen unpublished data). For significant main effects, e.g., among-site differences, pairwise tests with Bonferroni correction were performed to determine whether differences between pairs of sites were significant. For statistical analyses where at least one predictor variable

was continuous (cache size, plant size) and the response variable was binary or binomial, we employed a design with cache as the experimental unit. For cache survival, we used logistic regression (SAS Proc Logistic), while for seedling survival within caches, we used binomial regression with the response variable expressed in the events/trials format (SAS Proc Glimmix). To examine seedling survival during each inter-census period as a function of precipitation during that period, we used binomial regression with ending and starting seedling numbers for each inter-census interval at each site expressed in the events/trials format, with site and inter-census interval categorical predictor variables and precipitation deviation from the mean at each site during each inter-census interval as a continuous variable (SAS Proc Glimmix). Plant size data were analyzed using analysis of variance (SAS Proc GLM); data were transformed as necessary to meet distribution assumptions.

We analyzed rodent trapping data at each site by first expressing the total number of nocturnal granivorous rodents captured in terms of their relative abundance at the generic level, i.e., proportion of kangaroo rats (*Dipodomys* spp., Heteromyidae), pocket mice (*Perognathus* spp., Heteromyidae), deer and pinyon mice (*Peromyscus* spp., Cricetidae) and wood rats (*Neotoma* sp., Cricetidae). We then tested the hypothesis that first-year seedling survival would be negatively correlated with *Dipodomys* relative abundance.

3. Results

3.1. Seedling emergence

A majority of blackbrush seedlings in both intact stands and on disturbances emerged in clusters from rodent caches, with mean number of seedlings per cache varying from 2.7 to 7.4 (Table 2). Emergence was essentially complete by mid-March, as very few newly emerged seedlings were observed after the initial tagging. Initial density varied from 0.21 to 3.1 caches-m⁻² and from 0.9 to 10.2 seedlings-m⁻². There were significant differences among sites in both cache density ($\chi^2 = 530$, df = 3, $P < 0.0001$) and seedling density ($\chi^2 = 1966$, df = 3, $P < 0.0001$) in intact stands (Toquerville > Little Rockies > Salt Valley > Hurricane for cache density; Toquerville = Little Rockies > Salt Valley > Hurricane for seedling density). Disturbances had significantly lower cache and seedling densities than adjacent intact stands overall (disturbance main effect for cache density: $\chi^2 = 118.2$, df = 1, $P < 0.0001$; disturbance main effect for seedling density $\chi^2 = 530$, df = 3, $P < 0.0001$), but the site by disturbance interaction was also significant for both variables (cache density: $\chi^2 = 76.1$, df = 2, $P < 0.0001$; seedling density: $\chi^2 = 300$, df = 3, $P < 0.0001$). Cache density was lower on disturbances to some degree at all three sites, but seedling density was lower on disturbances only at Toquerville and Salt Valley (Table 2).

The distribution of seedlings among caches of different sizes was generally similar across sites, with a modal cache size category of 2–5 seedlings (Table 3). Cache size distribution in intact stands

Table 3
Cache size (initial seedling number per cache) distribution in intact stands at four blackbrush sites and on disturbances at three of the sites.

Site/disturbance	% Of caches in each cache size category				
	1	2–5	6–10	11–15	>15
Salt Valley					
Intact stand	24.6	35.4	22.3	11.8	5.9
Disturbance	15.5	38.0	22.5	15.0	9.0
Little Rockies					
Intact stand	23.5	38.0	14.7	14.0	9.8
Hurricane					
Intact stand	51.3	36.3	9.7	2.4	0.3
Disturbance	7.9	31.4	33.6	20.7	6.4
Toquerville					
Intact stand	28.1	55.7	13.9	1.7	0.6
Disturbance	25.0	55.2	18.4	0.7	0.7

differed among sites ($\chi^2 = 260.1$, $df = 12$, $P < 0.0001$), and all pairwise comparisons among sites were significant. The difference was most marked for Hurricane, where the smallest cache size was strongly over-represented. Large caches in intact stands were under-represented at both Hurricane and Toquerville relative to the other two sites. When cache size distributions in intact stands vs. disturbances were compared, there were no significant differences at Toquerville and Salt Valley, but at Hurricane, small caches were under-represented on the disturbance relative to the intact stand ($\chi^2 = 155.2$, $df = 4$, $P < 0.0001$).

More seedling caches in intact stands were located in the open (combined category including open, adjacent to blackbrush, and adjacent to other perennials) than under the crowns of perennials (Fig 1). When the observed number of caches under blackbrush crowns was compared with the expected number of caches based on blackbrush cover at each site, there was a significant difference among sites (site $\times$ position interaction: $\chi^2 = 40.3$, $df = 3$, $P < 0.0001$). Pairwise tests showed that at Salt Valley, Toquerville, and Hurricane, caches were significantly and equally under-represented under blackbrush crowns, whereas at Little Rockies caches were significantly over-represented under blackbrush crowns.

3.2. Seedling first-year survival

Seedling first-year survival in intact stands differed significantly among sites ($\chi^2 = 3768$, $df = 3$, $P < 0.0001$; Little Rockies $\gg$ Salt Valley $>$ Toquerville $>$ Hurricane) and ranged from 1 to 75% (Fig 2). At Little Rockies, 91% of caches still contained at least one seedling

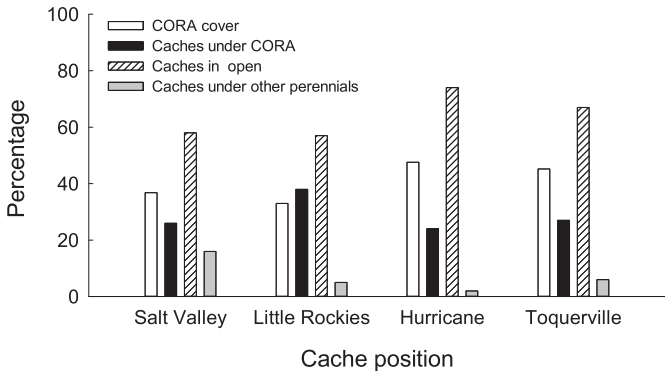


Fig. 1. Percentage of caches located under blackbrush (CORA) crowns, in the open, and under the crowns of other perennials in intact stands at each of the four study sites. The first bar for each site shows blackbrush cover percentage.

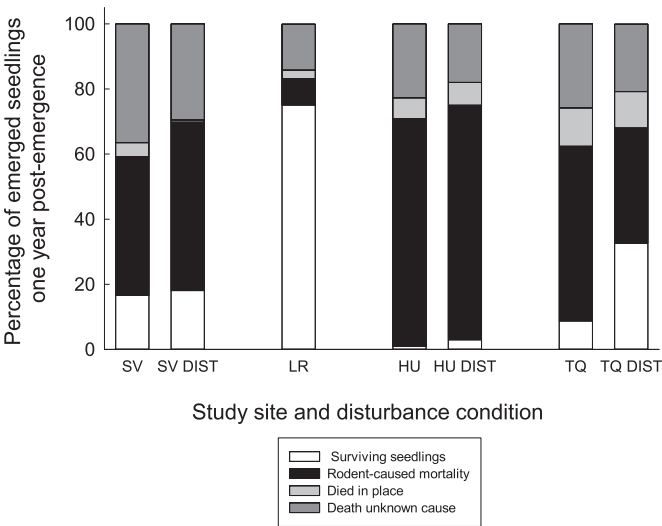


Fig. 2. Percentage of seedlings that survived the first year or that suffered mortality from causes related to rodent predator activity (excavation and herbivory), from causes that left the plants standing in place, or from unknown causes in intact stands at four sites and on disturbances at three of the sites. SV = Salt Valley, LR = Little Rockies, HU = Hurricane, TQ = Toquerville.

after a year, whereas at Hurricane only 2% of caches still contained at least one seedling. First-year seedling survival was significantly higher on disturbances than in adjacent intact stands ($\chi^2 = 431.9$, $d.f. = 2$, $p < 0.0001$; Fig 2).

The principal cause of first-year mortality was rodent activity, either through excavation of emerged caches or through direct seedling predation (Fig 2). Rodent trapping data provided circumstantial evidence that kangaroo rats (genus *Dipodomys*) likely caused most of the seedling mortality, as relative abundance of kangaroo rats was significantly negatively correlated with first-year seedling survival across sites (Fig. 3; $r = 0.974$, $df = 2$, $p = 0.026$). At sites with high relative abundance of kangaroo rats, confirmed

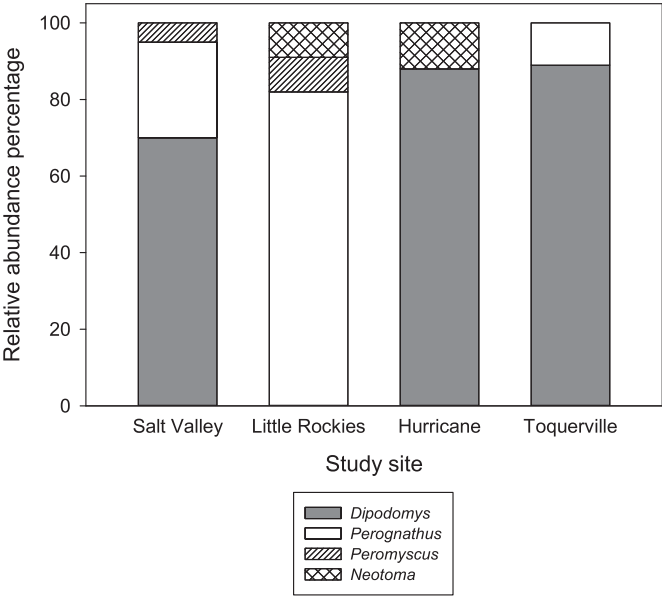


Fig. 3. Relative proportion of granivorous nocturnal rodents trapped during two nights in spring/summer 1997 at four sites that belonged to the genus *Dipodomys* (kangaroo rats), *Perognathus* (pocket mice), *Peromyscus* (deer and pinyon mice) and *Neotoma* (wood rats).

rodent-caused seedling mortality ranged from 43 to 70%, and an additional 24–36% of seedlings disappeared, probably also due to predation. A very different pattern was seen in the intact stand at Little Rockies, the site where a pocket mouse was the only heteromyid present. Only 8% of the seedlings suffered rodent-caused mortality and only an additional 14% disappeared.

There was a trend across sites for higher seedling mortality in larger caches in intact stands during the first year ($F = 14.06$, $d.f. = 1, 1313$, $p = 0.0002$). The magnitude of the effect varied among sites (site $\times$ cache size interaction: $F = 3.99$, $d.f. = 2, 1313$, $p = 0.0188$; Toquerville $\gg$ Little Rockies $>$ Salt Valley). Seedling mortality increased from 10% in single-seedling caches to 85% in caches with >10 seedlings at Toquerville, where the effect was most apparent. Hurricane was not included because of mortality $>98\%$ across all cache sizes.

Seedling survival from first to second census varied as a function of position relative to blackbrush crowns in intact stands at three sites, and these differences persisted at least through the second year (Fig 4). Site by position interactions were significant at the

second census ($\chi^2 = 150.2$, $df = 2$, $p < 0.0001$) and also after one and two years ($\chi^2 = 56.28$ after one year, $\chi^2 = 50.71$ after two years, $d.f. = 2$, $p < 0.0001$). At Salt Valley and Toquerville, survival from first to second census was lower in the open than under blackbrush crowns, while at Little Rockies, survival was significantly higher in the open. Pairwise tests showed that the effect of position at Little Rockies was always significantly different than at the other two sites, but Toquerville and Salt Valley were only significantly different from each other at the second census, when the protective effect of blackbrush crowns much stronger at Toquerville. Subsequent mortality under blackbrush crowns was somewhat higher at Toquerville than at Salt Valley, so that the net effect of position became similar at the two sites after one and two years.

Survival differences due to position are probably related to differential rodent activity, as most of the mortality occurred within the first six weeks and was rodent-caused. This was the primary cause of differential survival under blackbrush versus in the open over a two-year period, as evidenced by the nearly parallel survival time courses after the first six weeks at Little Rockies and Salt Valley (Fig. 4). At Toquerville there was some evidence for a small negative impact on post-seedling survival under blackbrush crowns, presumably due to adult competition.

3.3. Long-term juvenile survival

Juvenile survivorship curves generally showed a pattern of declining mortality risk with increasing age (Fig 5). At Salt Valley and Toquerville, there was a generally flattening trend in survival through the remaining seven years of the study, and some tagged members of the 1992 cohort survived for the full nine growing seasons, even in intact stands. Long-term survival was substantially higher on pipeline disturbances at these two sites.

The pattern of long-term survivorship at Little Rockies was again different from the pattern at the other sites (Fig 5). After initial first-year mortality, there was very little additional mortality during the subsequent two growing seasons (through fall 1994). Nine-year seedling survival in the intact stand at Little Rockies (27%) was much higher than at the other two sites with long-term data ($<1\%$). Long-term seedling survival even on pipeline disturbances at these two sites (7% at Salt Valley and 9% at Toquerville) was much lower than survival in the intact stand at Little Rockies, where 54% of the caches still contained at least one seedling after nine years.

The higher long-term survival at Little Rockies was not just due to lower first-year mortality. If seedling survival in intact stands after nine growing seasons is expressed as a percentage of the seedlings that survived one year, site differences were still highly significant ($\chi^2 = 155.8$, $d.f. = 2$, $p < 0.0001$), with much higher seedling survival at Little Rockies (35.3%) than at Salt Valley and Toquerville (5.4 and 5.7%, respectively). Survival values expressed in these terms at Little Rockies were more similar to values for the pipeline disturbances at the other two sites (35.3% at Salt Valley and 29.4% at Toquerville). Survival from one to nine years was significantly higher on pipeline disturbances than in intact stands at these sites ($\chi^2 = 73.7$, $d.f. = 1$, $p < 0.0001$).

Deviation from mean precipitation during five inter-census periods at each site over nine years was used as an index of moisture availability. Analyses relating this index to juvenile survival during each census period failed to reveal any significant relationship. Site had a significant effect on mean inter-census survival ($F = 233.18$, $d.f. = 2, 1$, $p = 0.0423$), which averaged 79% at Little Rockies, 49% at Salt Valley, and 42% at Toquerville. Overall, the first census interval had a large positive precipitation deviation (much wetter than average), while the other intervals experienced near-average precipitation. All four post-establishment census intervals at Little Rockies experienced moderate negative deviations from

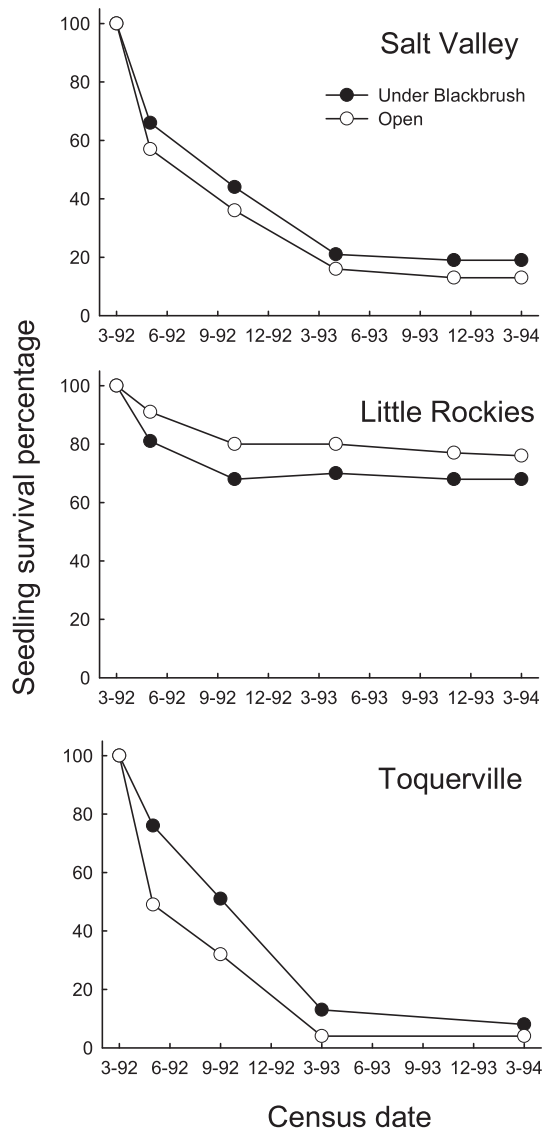


Fig. 4. Blackbrush seedling survival during the first two years following the initial census for seedling caches located under blackbrush crowns versus those located in the open interspaces in intact stands at three sites.

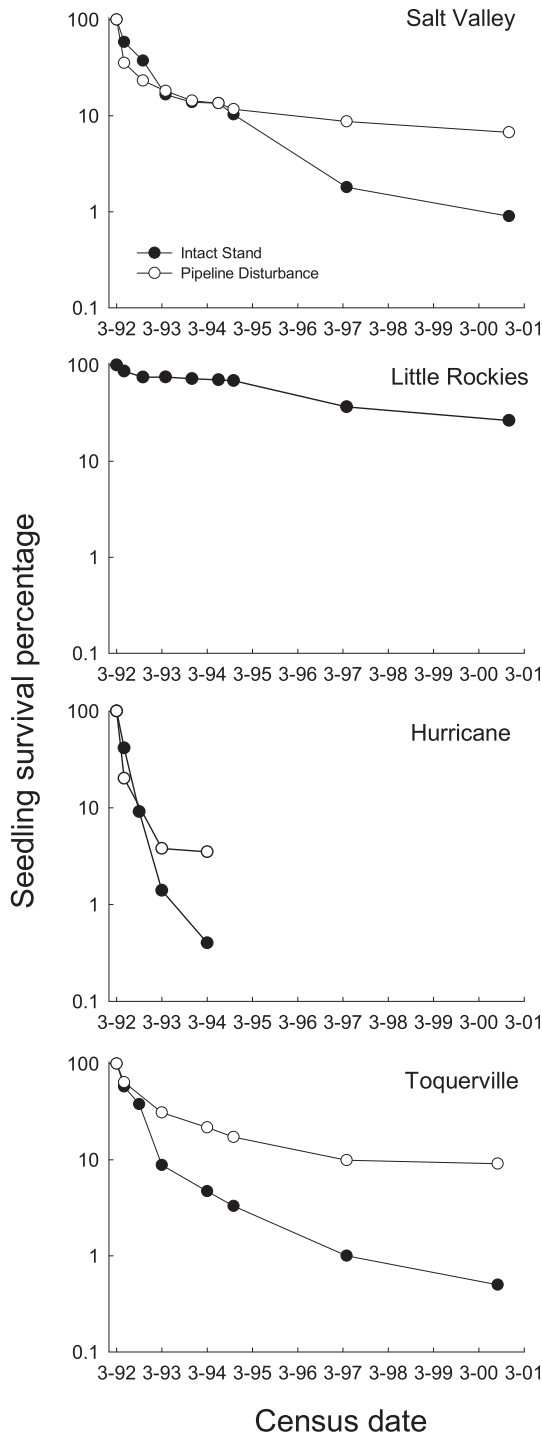


Fig. 5. Blackbrush seedling survival over nine growing seasons following emergence in spring 1992 in intact stands (black circles) at four sites and on pipeline/road disturbances (white circles) at three of the sites. Development at the Hurricane study site prevented data collection beyond two years.

the mean (drier than average), while both Salt Valley and Toquerville experienced average or above average precipitation in at least three of these four intervals. These results indicate that the dramatically higher long-term seedling survival at Little Rockies was not due to a more favorable precipitation regime.

Analysis of long term survival patterns as a function of position and cache size was possible only at Little Rockies. Nine-year

seedling survival was lower under blackbrush crowns than the open (21 vs. 31% survival; $\chi^2 = 34.7$, d.f. = 1, $p < 0.0001$). This difference was an extended consequence of higher rodent-caused seedling mortality under blackbrush plants in the first six weeks, which accounted for a 10% decrease in seedling survival underneath blackbrush crowns relative to open spaces (Fig 5). This survival difference could therefore not be credited to the competitive effects of adult plant crowns.

Long-term survival at Little Rockies as a function of initial cache size showed contrasting patterns for cache survival and seedling survival. Individual seedlings showed a pattern of decreasing survival with increasing cache size, with seedlings in the largest caches less than half as likely to survive as single seedlings ($F = 40.20$, d.f. = 1, $p < 0.0001$). The converse was true for cache survival; caches with >5 seedlings initially were 1.5 times as likely as the smallest caches to contain at least one surviving seedling after nine years (Wald $\chi^2 = 14.7$, d.f. = 1, $p < 0.0001$). The probability of cache persistence was uniformly high for all but the two smallest initial cache size categories.

3.4. Juvenile growth

When seedling size was quantified after three growing seasons, the plants were still remarkably small (Fig 6). Mean height of the tallest seedling in a cache ranged from 4 to 6 cm while mean stem diameter ranged from 0.8 to 1.7 mm. Plants in intact stands were taller and had thicker stems at Toquerville than at the other two sites. Little Rockies plants had significantly thinner stems than Salt Valley plants. At Salt Valley, plants on the pipeline were significantly taller and thicker-stemmed than plants in the intact stand. At Toquerville the plants were not significantly different in height but pipeline plants had slightly thicker stems.

When plant size was again quantified after nine growing seasons, the height differences among sites and disturbance regimes were much more pronounced (Fig 7). At Little Rockies there was no significant increase in the height of the tallest plant in a cache over the 6-year period (1994 height of 9-year survivors used for comparison); the mean increase in height was 0.6 cm (4.7–5.3 cm). Survivors in intact stands at Toquerville and Salt Valley were significantly taller than those at Little Rockies. Survivors on pipeline disturbances were significantly taller than those in intact stands (17.3 vs. 11 cm at Toquerville and 13.7 vs. 8.3 at Salt Valley). Both mean crown and stem diameter of Toquerville pipeline plants in 2000 were significantly greater than those of plants in intact stands (crown diameter 17.8 vs. 7.9 cm, $F = 11.41$, d.f. = 1, 29, $p = 0.0021$; stem diameter 8.9 vs. 6.1 mm, $F = 5.47$, d.f. = 1, 29, $p = 0.0265$). Crown diameter at Salt Valley was also significantly greater for pipeline plants (13.2 vs. 5.8 cm, $F = 12.74$, d.f. = 1, 57, $p = 0.0007$). Stem diameter was not formally quantified at Salt Valley or Little Rockies in 2000, but notes indicated that the maximum stem diameter observed at Little Rockies was <3 mm. In the most year of 2001, we observed tagged plants on the Salt Valley pipeline in flower, whereas no individuals of the 1991 cohort in the intact stand there were large enough to flower (S. Meyer, personal observation).

Plant size at three years was not a strong predictor of survival to nine years, as neither mean nor maximum height of seedlings in a cache was significantly related to cache survival. The only growth parameter that had any predictive power in terms of long-term survival in intact stands was mean stem diameter (Wald $\chi^2 = 6.18$, d.f. = 1, $p = 0.0129$). In an analysis of the effect of growth parameters on survival for two sites with two disturbance regimes, mean stem diameter was again the only significant predictor of cache survival (Wald $\chi^2 = 7.17$, d.f. = 1, $p < 0.0074$).

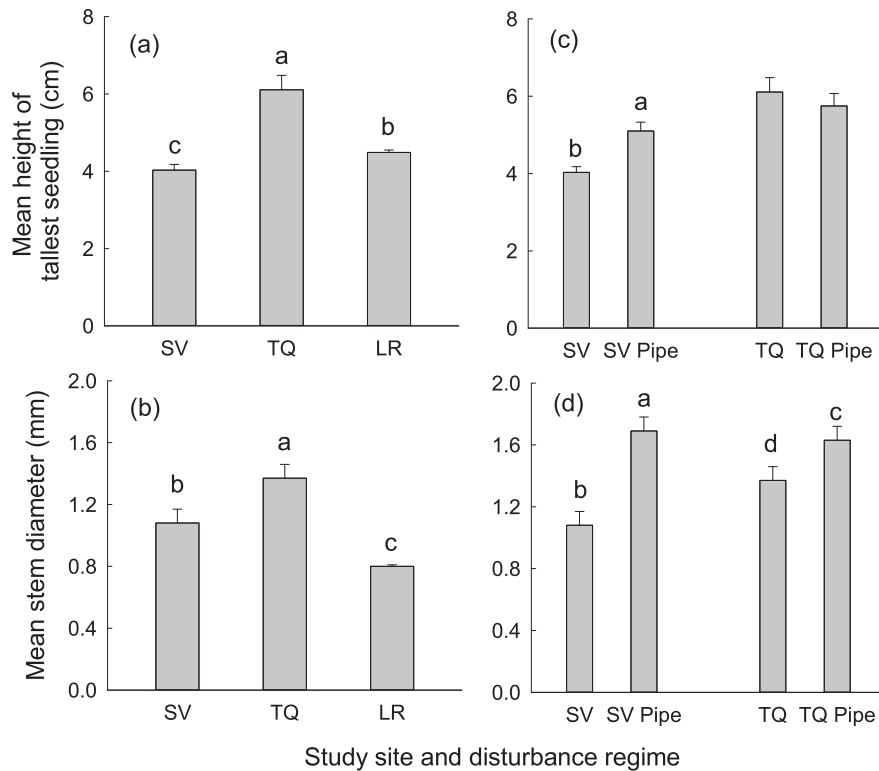


Fig. 6. Mean height of tallest seedling in a cache (a), and mean seedling stem diameter (b) for blackbrush seedlings in intact stands at three sites, and mean height of tallest seedling in a cache (c), and mean seedling stem diameter (d) for blackbrush seedlings in intact stands vs. pipeline disturbances after three growing seasons. Study sites: SV = Salt Valley, TQ = Toquerville, LR = Little Rockies. Error bars = standard error of the mean. Means within panels (a) and (b) and within sites in panels (c) and (d) that are headed by different letters are significantly different at $p < 0.05$ (Ismeans separations from Proc GLM SAS Version 9.4).

4. Discussion

4.1. Recruitment and early survival

This study has demonstrated the importance of heteromyid rodents to blackbrush regeneration ecology, both as seed dispersers and as seed and seedling predators. Blackbrush clearly fits the

model of a species that ‘manipulates the scatter-hoarding behavior of seed-dispersing animals’ as outlined by VanderWall (2010). It produces large, nutritious seeds that are valued as a food by heteromyid rodents, but these seeds impose handling costs in the form of slow husking time and secondary compounds that increase the probability of hoarding rather than immediate consumption (Auger, 2005). In order to gain the benefits of scatter-hoarded dispersal, blackbrush produces mast crops at intervals of several years, in order to potentially satiate predator demand (van der Wall, 2010). This adaptive syndrome involves trade-offs, however. Blackbrush relies on heteromyid rodents to disperse its seeds, but the rodents exact a large price for this service.

Seedling predation proved to be a major obstacle to blackbrush establishment, especially at sites where kangaroo rats were dominant, with known predator-caused mortality of 35–72%. Relatively high seedling predation may be common in desert systems (e.g., Beck and Vander Wall, 2010). Merriam’s kangaroo rats, the species at the Hurricane and Toquerville study sites, are specifically known to consume large amounts of green plant material in spring (Nagy and Gruchacz, 1994). It is not known for certain that kangaroo rats were the consumers of the seedlings in this study, but they were by far the most frequently trapped species where they occurred. The lower rodent-caused seedling mortality at Little Rockies could be associated with differences in behavior between kangaroo rats and the Great Basin pocket mouse that was the only abundant rodent there.

Several other differences in seedling demography between Little Rockies and the other sites could also be interpreted in terms of rodent behavior. At Little Rockies, caches were overrepresented under blackbrush plants, and caches under blackbrush plants suffered heavier rodent-caused mortality than those in the open. The

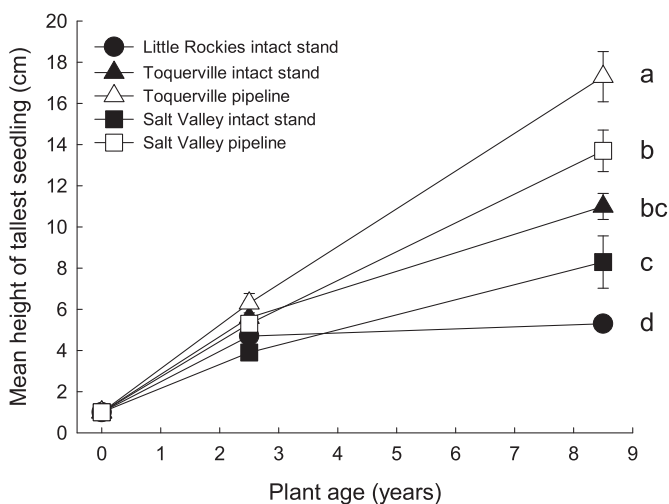


Fig. 7. Mean plant height of tallest seedling in a cache after three and nine growing seasons post-emergence in intact stands at three sites and on disturbances at two of the sites. Nine-growing-season means followed by the same letter are not significantly different at $p < 0.05$ (Ismeans separations from Proc GLM SAS Version 9.4).

reverse was true for Salt Valley and Toquerville, where caches were underrepresented under blackbrush plants, and seedlings in the open suffered heavier rodent predation. The propensity for pocket mice to seek cover and for kangaroo rats to prefer open ground is well established (Price and Brown, 1983). Also, there was very little mortality at Little Rockies due to seedling predation, suggesting that the pocket mice rarely engaged in this behavior. The rodent-caused mortality there was almost all incident to excavation. At the other sites, stem bases where seedlings had been chewed off were commonly encountered. The generally higher seedling mortality associated with larger caches was probably related to their greater attractiveness to consumers. The seedlings apparently became unattractive after the first season of growth, after they lost their succulence.

The combined effects of seed and seedling predation resulted in marked differences in initial recruitment among sites. Recruitment was lowest at Hurricane, where seedling density in the intact stand at the end of the first year was reduced to 1% of the original density of 0.9 seedlings-m⁻², or approximately one seedling-100 m⁻². At the other end of the spectrum was Little Rockies, where seedling density after one year was 75% of the original density of 9.7 seedlings-m⁻² or approximately 728 seedlings-100 m⁻². Most of this variation in initial recruitment was likely due to differential effects of the rodent communities at the different sites.

4.2. Long term survival and growth

Long term survival and growth rate were both significantly increased on small scale disturbances relative to intact stands at Toquerville and Salt Valley. This pattern strongly suggests release from the competitive effects of adult blackbrush plants on small-scale disturbances. This effect is commonly observed in desert systems, where successful recruitment into intact stands can be very rare, while recruitment in disturbed areas is often much more successful (Ackerman, 1979; Hunter, 1989). More generally, studies using neighbor analysis have frequently shown that perennial plants in deserts interact competitively even at wide spacings that eliminate the effects of competition for light (Fowler, 1986).

Studies of desert shrub demography have also detected strong differences in seedling survival and growth between under-crown and interspace positions in intact stands (McAuliffe, 1988; Miriti et al., 2001). Facilitation of seedling establishment under shrubs (the 'nurse plant' effect) is frequently reported, especially facilitation by a different species (e.g., McAuliffe, 1988; Franco and Nobel, 1989; Suzán et al., 1996; Butterfield et al., 2010). McAuliffe (1988) noted the occurrence of conspecific establishment facilitation, a phenomenon he called 'self-replacement' based on the idea that the juvenile plant would eventually replace the facilitating adult.

The effect of adult plants on recruitment and survival was site-dependent. At sites where kangaroo rats were the common rodents, blackbrush performed the apparently facilitative role of protection from herbivory (McAuliffe, 1986). In contrast, at the site where pocket mice were the common rodents, seedlings under blackbrush plants suffered an increase in rodent-caused mortality. These differences in mortality were evident after the first six weeks, the period when rodent activity had the most impact, and persisted for up to nine years. Juvenile plants under blackbrush crowns at Little Rockies were slightly taller and more slender than individuals in the open, but there were no other significant effects of blackbrush crowns versus open interspaces on long-term survival and growth in intact stands. The competitive effects exerted by adult plants on juveniles appeared to operate equally strongly under shrub crowns and in interspaces.

At Little Rockies nine-year survival was remarkably high (27%), while at the other sites, nine-year survival in intact stands was very

low (<1%), and survival even on disturbances was much lower than in the intact stand at Little Rockies (Fig. 6). Survival of one-year-old plants through eight additional growing seasons in intact stands was six times more likely at Little Rockies than at Salt Valley and Toquerville. Higher survival at Little Rockies was not explained by more favorable growing conditions, i.e., periods of above-average precipitation.

Another explanation for the large difference in survival between sites is that cache disturbance by rodents early in life has negative longer-term consequences for survival, and that the minimal disturbance by pocket mice at Little Rockies contributed to the high long-term survival there. This idea is supported by data from experimental work at Salt Valley (Meyer and Pendleton, 2005). Seedling survival in protected artificial caches on the pipeline was 89% after three years, with an average of 11 surviving juveniles per cache, even though the protective cages were removed after two growing seasons. Three-year survival in unprotected artificial caches was 39%, substantially higher than survival in natural caches on the pipeline (14%) but much lower than in protected caches. This higher survival in artificial vs. natural caches could have been because rodents are more likely to return to their own caches than to find artificial caches (Steele et al., 2011).

At the Hurricane site, the difference in artificial cache survival due to protection from seed predators (19% of emerged seedlings in protected caches vs. 0% in unprotected caches) was also evident (Meyer and Pendleton, 2005). Similar results were obtained by Jones et al. (2014) in a blackbrush establishment experiment in southern Nevada, in which protection from predation substantially increased both emergence and survival.

4.3. The masting adaptive syndrome

Mast seeding in mesic environments is associated with a specific seed and seedling adaptive syndrome. In his classic work on plant adaptive strategies, Grime (1979) cited regeneration involving a "persistent seedling bank" as the principal mode in stable forests of shade-tolerant trees, which are unproductive habitats with low intensities of disturbance, where self-replacement from the seedling bank follows gap formation resulting from the death of individual trees. Blackbrush stands could also be described as closed communities in unproductive habitats with historically low intensities of disturbance. Tachiki and Iwasa (2010) modeled the evolution of masting in the context of closed forest communities. They concluded that 'masting never evolves if all vacant sites (gaps) are filled by individuals from seeds produced in the same year, despite the fact that trees reproducing intermittently enjoy a higher pollination success than trees reproducing annually'. They also found that, in the absence of a persistent seed or seedling bank, the presence of seed predators could not promote the evolution of masting. In species with specialist pre-dispersal predators (e.g., insects), a persistent seed bank can perform the same function as a seedling bank (Rees et al., 2002), but when seed predation is post-dispersal, formation of a persistent seed bank would be under negative selection. This suggests that masting, predator satiation, a transient seed bank, and formation of a seedling bank that persists across years are associated traits that promote survival in closed stands with high levels of seed predation from post-dispersal predators.

The pattern of high juvenile survival and very slow growth observed in the intact blackbrush stand at Little Rockies and to a lesser extent at Toquerville and Salt Valley has demonstrated that blackbrush can form persistent seedling banks following recruitment after a mast year. The idea that slow seedling growth rates were caused by suppression due to root competition from adult plants was supported by faster growth rates that appeared to be

linear through time in the absence of adult competition, whereas in closed stands growth was slower and tended to be asymptotic (Fig 7). In addition, plant sizes for individuals from these four populations were quite similar after three years at wide spacing in a common garden, and approximated plant size after nine years on pipeline disturbances in this study (Richardson et al., 2014; B. Richardson unpublished data). This indicates that growth rate is plastic in this species, and that the very small size of nine-year-old plants in intact stands was due to a combination of biotic and abiotic stress that was directly analogous to the stress experienced by seedling banks in forests.

In order for masting to be advantageous for blackbrush, the ability to form seedling banks is an essential part of the associated establishment syndrome. The equivalent of gap formation would be the eventual senescence and death of older individuals, and this would not necessarily be associated with mast years or the establishment years that immediately follow. Self-replacement in clumps as well as occasional establishment in the interspaces of intact stands is probably the norm in this species. Clumps that appear to be single individuals are often comprised of several individuals of multiple ages (S. Kitchen unpublished data). The younger plants remain small, but intermediate-aged plants may be as large as the oldest plants, suggesting that when older plants die, younger plants may be able to increase their growth rates.

4.4. Conclusions

This study has demonstrated that dispersal in blackbrush is associated with heteromyid rodents that are also seed and seedling predators. They take a heavy toll on seeds and seedlings even following a mast year. In order to satiate predator demand, blackbrush has adopted a masting reproductive strategy along with seed traits that encourage caching behavior but also promote full first-year germination (Pendleton and Meyer, 2004). Juvenile plants experience strong suppression in intact stands but can exhibit relatively high survival by adopting a stress-tolerant strategy that includes very slow growth. Individuals in these 'seedling banks' likely respond with increased growth rates to gap formation in closed stands resulting from the death of adult plants. The pattern exhibited by blackbrush bears striking similarities to the adaptive syndrome exhibited by masting forest trees. This shows that the evolutionary forces that generate the masting adaptive syndrome in forests can also operate in desert shrublands.

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