



VIABILITY OF

Blackbrush seed (*Coleogyne ramosissima* Torr. [Rosaceae])

FOLLOWING LONG-TERM STORAGE

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ABSTRACT

Blackbrush (*Coleogyne ramosissima* Torr. [Rosaceae]) is a landscape-dominant shrub that occurs in an ecotonal band between warm and cold deserts of the western US. This vegetation type is at considerable risk from stand-replacing wildfires due to the introduction of exotic annual grasses. Because blackbrush does not form a persistent seedbank, restoration following fire requires that seed produced in past years be collected and stored for future use. This study examined germination of 32 collections of blackbrush seed following 12 to 27 y of storage at room temperature. Germination and emergence of multiple seed collections taken from across the geographic and elevational range of this species revealed that blackbrush seed can be maintained in storage for long periods of time. Average germination remained high (> 80%) for the first 10 to 12 y of storage. Emergence was low, however, when germination percentage fell below 50%, indicating that production from older seed may require that germinants be planted in a greenhouse

to produce plants for later outplanting to the field. Based on current climate predictions, blackbrush will likely migrate upward in elevation and (or) latitude as conditions become warmer and drier. Seed for restoration would best be used at the blackbrush upper elevational range or higher.

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KEY WORDS

emergence, germination, seed longevity, Mojave Desert, Colorado Plateau, restoration

NOMENCLATURE

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Figure 1. Blackbrush community in Arches National Monument, Utah, on the Colorado Plateau. Photo by Rhean Pendleton

Blackbrush (*Coleogyne ramosissima* Torr. [Rosaceae]) is the dominant landscape shrub on more than 3 million ha (7.4 million ac) of National Park Service, Bureau of Land Management, Navajo Nation, and Forest Service lands in the southwestern US. It occupies a transition zone between warm and cold deserts extending from the Colorado Plateau (Figure 1) through the Grand Canyon and into the boundary between the Mojave and Great Basin deserts (Figure 2). Blackbrush typically forms almost pure stands between mixed desert shrub communities at lower elevations and juniper-sagebrush communities at higher elevations (Bowns and West 1976). Seed of blackbrush is a primary source of food for desert granivores, particularly heteromyid rodents (Herrera and others 1998; Auger 2005). Mature shrubs provide browse for mule deer (*Odocoileus hemionus*) and desert bighorn sheep (*Ovis canadensis nelsoni*) (Bowns and West 1976).

Blackbrush communities are under threat from the combined effects of invasive grasses, increased fire frequency, and climate change. The introduction of exotic annual grasses into these communities has led to stand-replacing wildfires (Brooks and Matchett 2006; Brooks 2009). Blackbrush is highly flammable and does not resprout following fire. Once removed, the

subsequent community is most often dominated by annual grasses (*Bromus* L. spp. [Poaceae] and *Schismus* P. Beauv. spp. [Poaceae]) that are prone to recurring fire (Bowns 1973; Brooks and Matchett 2006). Given the increasing number of fires and short return intervals, recovery of long-lived desert species such as blackbrush in the absence of assisted restoration is unlikely (Abella 2009; Brooks 2009).

New recruitment in blackbrush is episodic and occurs solely through seed. Blackbrush does not form a persistent seedbank, and recruitment is dependent on the presence of seed produced the previous summer (Meyer and Pendleton 2005). Occasional mast seed crops, produced when environmental conditions and plant resource status are favorable (Figure 3), are followed by several years of minimal seed output (Pendleton and others 1995). Restoration of blackbrush communities will require a readily available source of seed. Consequently, seed produced in mast years will need to be collected and stored for future use. Information on the longevity of blackbrush seed in storage, however, is lacking. This article highlights a study that examined germination and emergence of multiple collections of blackbrush seed following 12 to 27 y of storage.



Figure 2. Mojave Desert blackbrush community near the Mojave National Preserve, California. Photo by Rosemary Pendleton



Figure 3. Upper elevational blackbrush community showing mass flowering at Browse, Utah. Photo by Burton Pendleton

MATERIALS AND METHODS

In 1991 and 1997, we collected seed (achenes) from multiple locations in the Colorado Plateau and Mojave Desert, representing the full geographic and elevational range of blackbrush (Table 1). In 1982, we purchased a commercial seedlot collected that same year in southern Utah, which had been stored in a warehouse prior to purchase. A subsample of each seedlot was weighed. We tested germination immediately after collection, at various times during the first 8 y of storage, and again 12 y (for 1997 seed) or 18 y (for 1991 seed) after collection, using the same method each time. For germination, 5 replicates of 25 seeds each were placed in standard 100 × 15 mm (4 × 0.6 in) Petri plates between 2 circles of blue blotter paper (Anchor Paper Company, St Paul, Minnesota) moistened with tap water. Plates were sealed in plastic bags and chilled in the dark at 5 °C (41 °F) for 6 wk. Following chilling, plates were transferred to a growth chamber set at 5/15 °C (41/59 °F) on a 12-h cycle. The regime of moist chill followed by a germination temperature of 5/15 °C had previously been determined as optimal for a wide range of blackbrush populations (Pendleton and Meyer 2004).

Tap water was added to the blotters as needed to maintain moisture during the experiment. Germinated seed was counted and removed from the plates 1 to 2 times per wk. Seed was considered germinated if the radicle extended 5 mm or exhibited bending. Following the 6-wk germination period, viability of non-germinated seed in each plate was determined using cut test procedures (AOSA 1988). Seed filled with an intact, white, firm embryo was scored as viable. Following the initial germination tests, seed was stored in unsealed manila envelopes at room temperature.

At various times during the first 8 y of storage, 2 to 9 randomly selected collections were germinated to determine viability. Nine collections were germinated after 1 y of storage, 2 after 4 y, 4 after 5 y, and 7 after 8 y of storage. For each collection, we determined percentage loss of germination by subtracting current germination percentage from initial germination percentage and dividing the result by initial germination percentage.

During 2009–2010, we retested all seed collections to determine viability following long-term storage. We tested germination of 32 collections and emergence for 28 of the 32 collections

TABLE 1

Population location, elevation, and year of collection for the 32 collections of blackbrush seed used for viability studies.

Population	State	Elevation (m)	Latitude/longitude	Year of collection
MOJAVE GROUP				
C-1 Hurricane Industrial Park	Utah	976	37°09'N/113°17'W	1991
C-2 Legrand Heights	Utah	976	37°09'N/113°18'W	1991
C-4 Toquerville Road	Utah	1128	37°15'N/113°16'W	1991, 1997
C-3 Toquerville Pipeline	Utah	1159	37°16'N/113°17'W	1991
C-7 Hurricane Mesa	Utah	1170	37°08'N/113°16'W	1991
C-5 Winchester Hills	Utah	1189	37°13'N/113°37'W	1991, 1997
C-6 Snow's Canyon Rim	Utah	1235	37°14'N/113°37'W	1991
C-16 Browse turnoff	Utah	1259	37°21'N/113°16'W	1991, 1997
C-17 Kyle Canyon	Nevada	1280	36°17'N/115°25'W	1991
C-13 Potosi Pass Road	Nevada	1372	36°00'N/115°32'W	1991
C-25 Veyo Road	Utah	1402	37°16'N/113°38'W	1991
C-24 Beaver Dam	Utah	1450	37°05'N/113°51'W	1997
C-19 Lower Lee Canyon	Nevada	1585	36°24'N/115°32'W	1991
B-2 Washington County	Utah	Unknown	Unknown	1982
COLORADO PLATEAU GROUP				
C-11 E Hite turnoff	Utah	1280	37°48'N/110°18'W	1991
C-8 Mexican Hat Rock	Utah	1304	37°09'N/109°50'W	1991
C-20 Gemini Bridges turnoff	Utah	1341	38°34'N/109°35'W	1991
C-26 North of Hanksville	Utah	1356	38°47'N/110°27'W	1991
C-23 South of Bluff	Utah	1402	37°15'N/109°44'W	1991
C-10 Bridges Road MM57	Utah	1402	37°45'N/110°16'W	1991
C-21 Arches National Park	Utah	1463	38°43'N/109°32'W	1991, 1997
C-27 Dirty Devil turnoff	Utah	1494	38°38'N/110°36'W	1991, 1997
C-22 White Mesa	Utah	1524	37°30'N/109°29'W	1991
C-9 Bridges Road MM68	Utah	1524	37°40'N/110°13'W	1991
C-12 Needles District	Utah	1535	38°08'N/109°46'W	1991
C-28 Little Rockies Bullfrog Road	Utah	1646	37°47'N/110°39'W	1991
C-29 Island in the Sky	Utah	1866	38°35'N/109°47'W	1991

(some were not tested for emergence because seed quantities were too limited).

Emergence was tested because older seed that germinates may not have sufficient vigor to emerge once sown. For emergence, we sowed a group (cache) of 3 seeds into each of 49 Ray Leach Cone-tainers (164 ml [10 in³]; Stuewe and Sons, Tangent, Oregon) filled with Sun Gro Metro-Mix 360 (Sun Gro Horticulture, Bellevue, Washington), for a total of 147 seeds per collection. In the wild, seed emerges in clusters from scatter-

hoard caches made by heteromyid rodents. Cone-tainers were watered to field capacity and incubated in a growth chamber at 5 °C (41 °F) for 6 wk, after which the chamber was reset to 5/15 °C (41/59 °F) on a 12-h cycle. Emergence was followed weekly until no new seedlings emerged, approximately 10 wk in total.

Emergence and germination percentages were analyzed by fitting a Generalized Linear Mixed Model (GLIMMIX) with a binomial distribution and logit link function using SAS v. 9.2 (SAS Institute 2007). Data from the 27-y-old seedlot from

Washington County, Utah, were not included in the statistical analyses as it was the only collection from that year. Explanatory variables were collection year (1991 or 1997), population group (Mojave or Colorado Plateau), and their interaction. Number of days to 50% germination or emergence was determined by fitting a curve to a graph of total germination or emergence against number of days since the experiment began. Rate data were analyzed by fitting a GLIMMIX with an exponential distribution and log link function. Explanatory variables were collection year, population group, and elevation of collection site with interactions. Average seed weight was analyzed by fitting a GLIMMIX with a lognormal distribution and identity link function. Explanatory variables were collection year, population group, and elevation. All models included a repeated measure component that assumed a first-order, autoregressive relationship between residuals across different years. A Tukey-Kramer adjustment was made for multiple comparisons. Correlations were graphed using Microsoft Office Excel 2007.

As reported in other seed longevity studies (for example, Ellis and Roberts 1980; Bebawi and others 1984), blackbrush seed viability decreased with storage time (Figure 4). Total germination percentage and germination rate were significantly lower for the 18-y-old 1991 seed collections as compared with the 12-y-old 1997 collections ($P = 0.0060$ and < 0.0001 , respectively). The seed age $\times$ population group (Mojave or Colorado Plateau) interaction term was significant for total germination and germination rate ($P = 0.0235$ and 0.0015 , respectively). The 12-y-old 1997 Mojave collections had, by far, the highest mean germination rate and total, significantly greater than the 1997 Colorado Plateau collections. In contrast, the 18-y-old 1991 Mojave and Colorado Plateau collections were not significantly different for any of the response variables (Figure 4). The winter preceding the 1997 Mojave flowering season was particularly wet, receiving 46 to 53 mm (1.8 to 2.1 in) of precipitation above the long-term average, whereas winter precipitation in

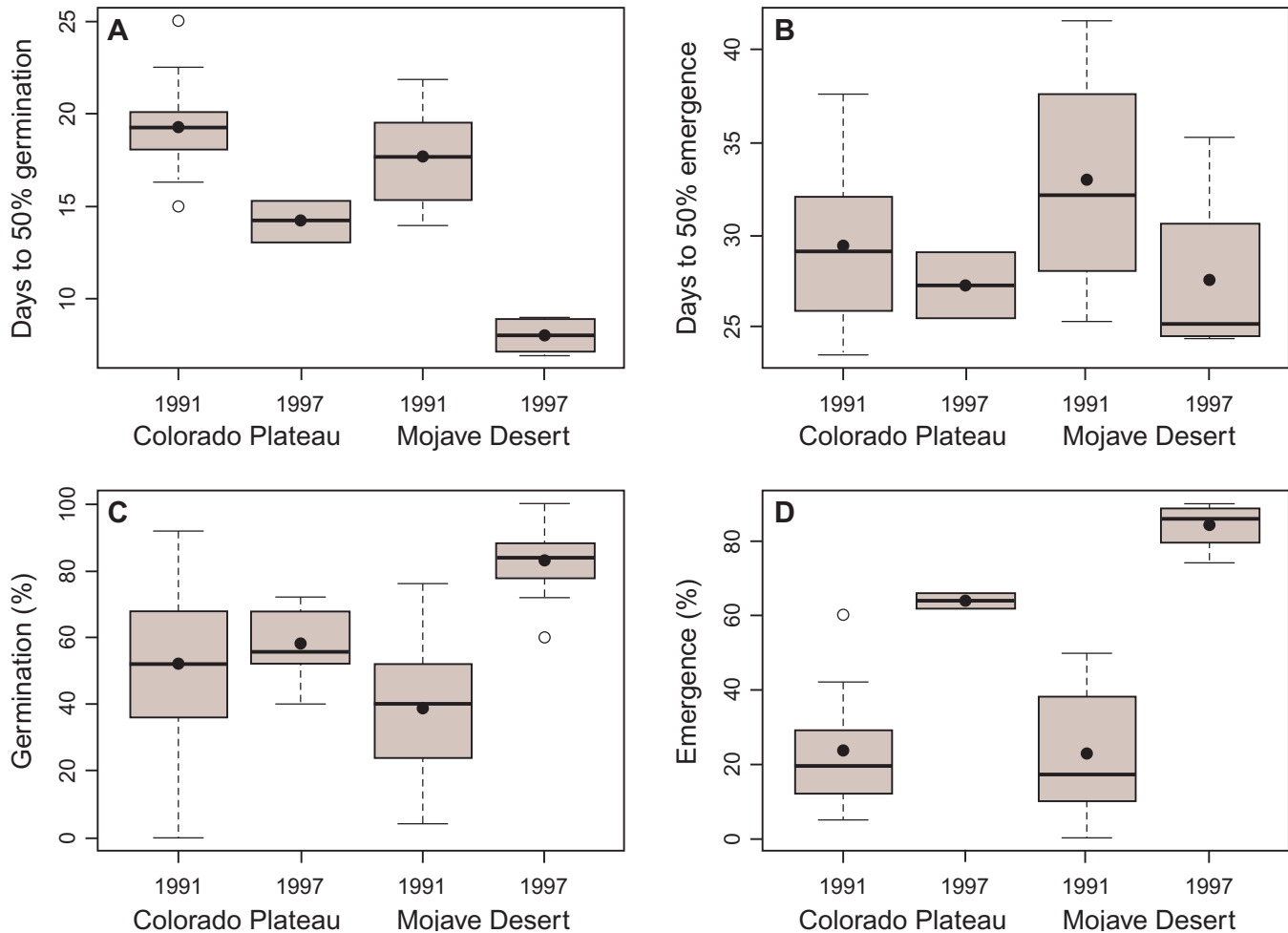


Figure 4. Box plots showing the mean (dots), median (heavy lines), and variation in days to 50% germination (A), days to 50% emergence (B), germination percentage (C), and emergence percentage (D) for Colorado Plateau and Mojave Desert seed collections. The bottom and top of the box represent the 25th and 75th percentile. Dashed lines encompass the range. Open circles represent outlier data points.

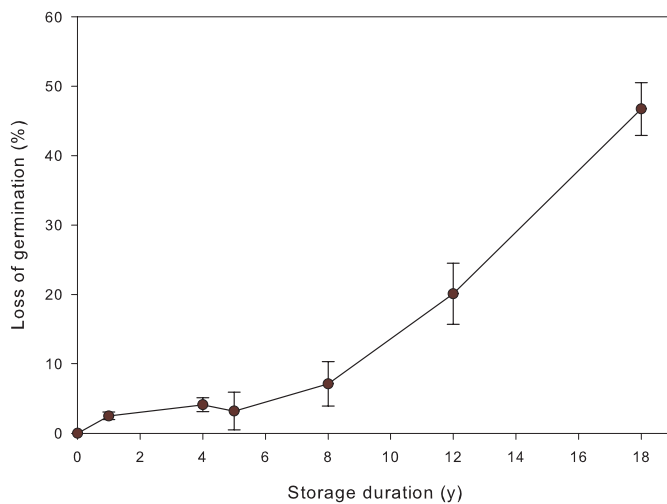


Figure 5. Loss in germination percentage with time in storage. Loss was calculated individually for each collection by subtracting the germination percentage following years in storage from the initial germination percentage for that collection. Data shown represent 31 collections tested initially, 9 random collections tested after 1 y, 2 after 4 y, 4 after 5 y, 7 after 8 y, 6 after 12 y, and 25 after 18 y. Error bars indicate the standard error of the mean.

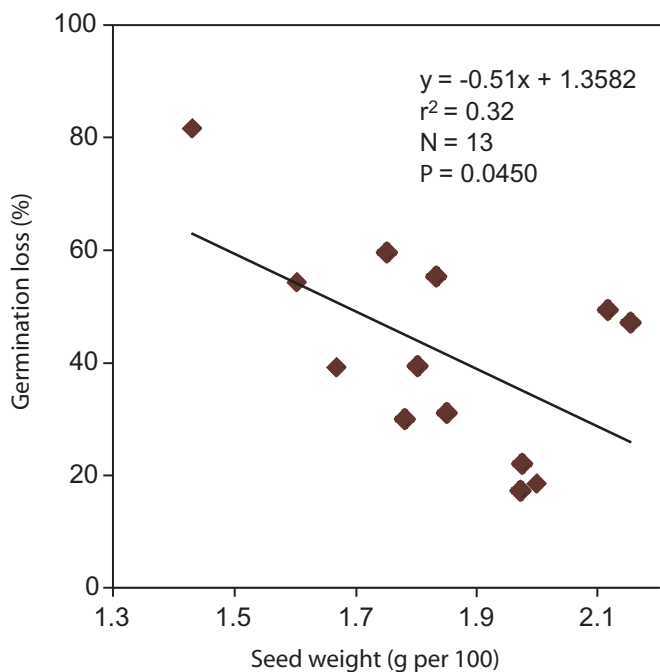


Figure 6. Relationship between seed weight and loss in germination percentage for 1991 Colorado Plateau collections.

the Colorado Plateau was closer to normal (data from the Western Regional Climate Center). The unusually wet winter may have contributed to the high quality of 1997 Mojave seed, as the maternal environment is known to affect seed provisioning, viability, and germination (Fenner 1991; Gutterman 2000). For example, high temperatures during seed fill and maturation decrease the viability of soybean seed (Keigley and Mullen 1986). Despite differences in germination rates, seed weight and emergence rate did not differ with either year or population group.

By combining the 12-y-old and 18-y-old seed germination data reported above with the periodic germination tests done after 1 to 8 y of storage, we were able to obtain an approximate estimate of loss in germination percentage over time (Figure 5). Average germination remained high (> 80% of the original) for the first 10 to 12 y of storage (Figure 5). Germination at the original time of collection ranged from 72 to 100%, with a mean of 89.8%. Loss in percent germination averaged from 0.03% after 1 y to 46.6% after 18 y. This result is comparable to seed storage data from other rosaceous shrubs. For example, Stevens and co-workers (1981) found no significant loss in germination of *Amelanchier* Medik., *Cercocarpus* Kunth, and *Purshia* DC. ex Poir. spp. following 7 to 15 y of storage in an open warehouse.

Variation in germination percentage among collections increased as the seed aged. The coefficients of variation (CV) for fresh seed, 12-y-old 1997 seed, and 18-y-old 1991 seed were 6.6, 17.9, and 40.8, respectively. Some of the difference in CVs reflects the number of collections used in the calculation—25 for fresh and 18-y-old seed versus only 6 for 12-y-old seed—however, variation among the older 1991 collections ($n = 25$) was substantial. Germination of the 1991 collection from the Bridges Road MM57 decreased from 95% at the time of collection to 78.6% after 18 y of storage. In contrast, germination of the 1991 Hurricane Industrial Park collection decreased from 93% to only 13.2% after 18 y of storage. In the Colorado Plateau, viability loss was related to seed weight (Figure 6), with small seed losing viability faster than heavy seed. No such relationship was found for Mojave Desert collections, where correlations between viability loss and precipitation in the winter preceding collection, elevation, and seed size failed to show any discernable pattern.

Elevation was marginally significant ($P = 0.0501$) in predicting germination rate. Lower elevation collections took less time to germinate (Figure 7). This same relationship was reported in the first germination experiment (Pendleton and Meyer 2004) and apparently was retained through the storage period. Seed from lower elevations also tended to be heavier for Colorado Plateau collections (Figure 8). Lower, more arid locations may need to respond faster to a limited window of opportunity for germination and growth. A number of studies

have shown that larger seed germinates and emerges at a higher rate than smaller seed (Dalling and Hubbell 2002; Benard and Toft 2008). Baker (1972) looked at seed weights of all taxa in the California flora and found that average seed weight was higher for herbaceous taxa whose seedlings were at risk of drought soon after establishment, thereby allowing for faster root development. Our data support this finding as elevation, seed weight, and germination rate were all correlated for Colorado Plateau populations.

Seed viability was also tested through emergence trials. Results of the emergence trials differed somewhat from those of the germination experiments. While total emergence percentage was significantly lower for the older 1991 seed collections as compared with 1997 collections ($P = 0.0112$), emergence rate did not differ with either year or population group (see Figure 4). The number of days for 50% emergence averaged a close 27.4 and 30.3 for 12-y-old and 18-y-old seed, respectively. Variation among collections in emergence rate was also much higher than those for germination rate.

We also tested the 27-y-old seedlot collected from Washington County, Utah, for germination and emergence. Original viability is not known, but 86% of the seed germinated 15 y after collection and 25.6% of the seed germinated following 27 y in storage (9 y of warehouse storage and an additional 18 y at room temperature). Germination rate for this collection was very slow, averaging 26.5 d to 50% germination, as compared with 9.8 d for 12-y-old 1997 seed and 18.5 d for 18-y-old 1991 seed. Although vigor of the 27-y-old seed was insufficient for successful emergence, planting germinants in a nursery may be an option for producing desired seedlots with low vigor (Luna and others 2008).

These data document differences in germination requirements for seed collected from the Mojave Desert and the Colorado Plateau. Climatic conditions in the 2 areas differ: the Mojave receives most of its moisture from January to March in the form of rain, whereas the Colorado Plateau receives more moisture during summer to early fall (Comstock and Ehleringer 1992). Average daily temperatures in the Mojave are 3 to 5 °C (5.5 to 10 °F) higher than those in the Colorado Plateau, based on long-term averages of 6 weather stations per area (data from the Western Regional Climate Center). These patterns may explain the greater recruitment success observed in Colorado Plateau populations (Meyer and Pendleton 2005).

MANAGEMENT IMPLICATIONS

This study demonstrated that blackbrush seed can be maintained in storage at room temperature for relatively long periods of time. Germinability of stored blackbrush seed remains high (> 80%) for 10 to 12 y, and nearly 50% of the seed germinated after 18 y. Germination rates slow, however, as seed ages

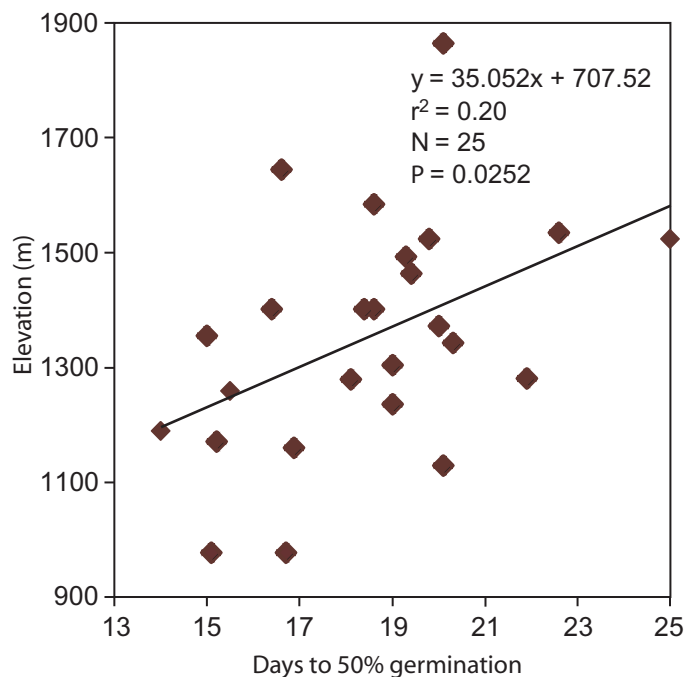


Figure 7. Relationship between elevation and germination rate for all 1991 seed collections.

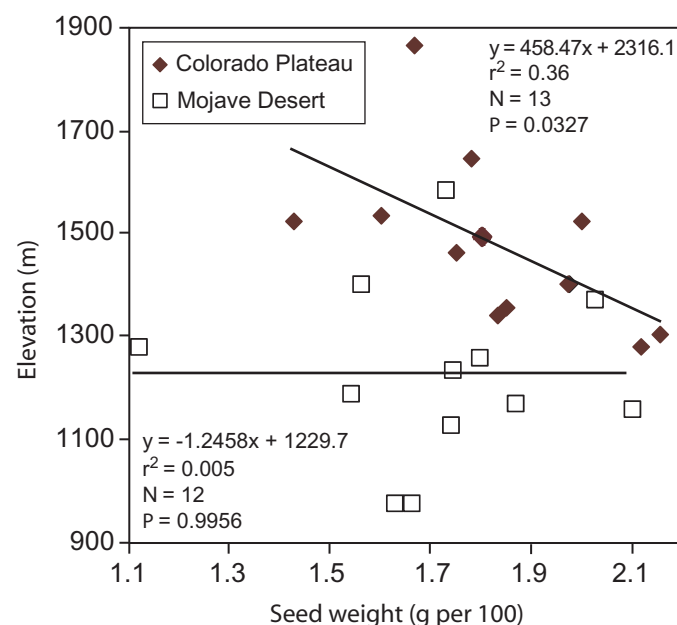


Figure 8. Relationship between elevation and seed weight for 1991 Colorado Plateau and Mojave Desert collections.



Figure 9. Seedlings emerging from a heteromyid rodent cache. Photo by Burton Pendleton

and, in this study, emergence was greatly reduced by 18 y post-collection. Consequently, older seed may require that germinants be planted in a greenhouse to produce plants for later outplanting to the field. (We produced plants from 27-y-old seed using this method.) Viability may well be longer if seed is stored at lower temperatures. Viability may also be affected by other storage factors such as container size and type.

Availability of stored seed may be increasingly important as plant ranges shift in response to predicted changes in climate. Data from pack rat middens indicate that the *Larrea/Coleogyne* ecotone moved 50 to 100 m (164 to 328 ft) downslope during the Little Ice Age (approximately 500 y BP) in response to increased winter precipitation and lower soil temperatures (Cole and Webb 1985; Hunter and McAuliffe 1994). Current climate change models project an upward shift of that ecotone on a similar or greater scale in response to warmer and dryer conditions (Rehfeldt and others 2006). Restoration of the blackbrush community at lower elevations in the Mojave Desert is not recommended as conditions in these areas favor *Larrea* Cav. establishment. Instead, blackbrush seed would best be utilized at the upper edge of its elevational range or possibly higher. Seedlings may also survive better when planted in clusters (Figure 9), mimicking naturally occurring rodent caches (Howe 1989) (Figure 9).

Mast crops of blackbrush can be detected well in advance of seed ripening and can be collected and stored for future restoration needs. A community-wide volunteer seed collection project was organized in southern Nevada in 2007, resulting in the collection of several hundred pounds of high-quality seed

(Brean 2008) for use in the restoration of burned areas. Proper storage of such volunteer-collected seed should provide an adequate seed source for future restoration projects.

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