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Original Research

Evaluating a Seed Technology for Sagebrush Restoration Across an Elevation Gradient: Support for Bet Hedging☆,☆☆

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ABSTRACT

Big sagebrush (*Artemisia tridentata* Nutt.) restoration is needed across vast areas, especially after large wildfires, to restore important ecosystem services. Sagebrush restoration success is inconsistent, with a high rate of seeding failures, particularly at lower elevations. Seed enhancement technologies may overcome limitations to restoration success. Seed pillows are one such technology designed to improve seed-soil contact in broadcast seedings by providing a favorable medium for seedling establishment and growth. Seed pillows have shown promising results in greenhouse studies; however, they have not been evaluated in the field. We compared broadcast-seeding seed pillows with broadcast-seeding bare seed in 2 yr across a large, burned elevation gradient. Compared with bare seed, we found no evidence that seed pillows improved sagebrush establishment and growth across the elevation gradient. Though our results suggest that seed pillows do not increase the likelihood of successful sagebrush restoration, they were successful at times when bare seeds were not, and the same was true for bare seeds. At least one of the two treatments was successful at 50% of the elevations over the 2 seeding yr. This suggests that a bet hedging approach, seeding both bare seed and seed pillows, may increase the probability of success. Further supporting the use of bet hedging, if both methods were used and seeding occurred in both years, success would have been 86%. Sagebrush density and cover varied by elevation. In the first-yr seeding, sagebrush density and cover generally increased with increasing elevation. In the second-yr seeding, sagebrush density and cover were greatest at the lowest and highest elevations. We speculate that at the lower elevations an unusually wet spring combined with limited herbaceous vegetation provided an ideal environment for sagebrush establishment and growth. Our results also demonstrate, counter to common assumptions, that lower elevations sagebrush seedings can be successful.

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Introduction

Sagebrush (*Artemisia* L.) restoration is needed across vast areas of the Intermountain West because it is a keystone species that provides important ecosystem services, such as habitat for sagebrush-obligate wildlife species (Crawford et al., 2004; Shipley et al., 2006; Prevéy et al., 2010). The sagebrush ecosystem is one of the most imperiled ecosystems in the United States, and its conservation is facing multiple threats (Noss et al., 1995; Davies et al., 2011). Sagebrush only occupies about 56% of its historic range and, in many areas, remaining sagebrush communities are highly fragmented (Knick et al., 2003; Schroeder et al., 2004). This loss of sagebrush habitat is a critical factor driving local sage-grouse *(Centrocercus urophasianus)* populations to extirpation (Aldridge et al., 2008) and has resulted in > 350 sagebrush-associated species being identified as species of conservation concern (Suring et al., 2005; Wisdom et al., 2005). Large wildfires in the past decade have further accelerated the loss of sagebrush and threatened sagebrush-obligate wildlife species.

Sagebrush restoration is needed, in particular after large wildfires, because natural recovery may take several decades to over a century (Baker, 2006; Ziegenhagen and Miller, 2009; Nelson et al., 2014). This time delay between disturbance and natural recovery can negatively affect sagebrush-obligate wildlife because these species often will not use the interiors of large burned areas until sagebrush recovers (Connelly et al., 2000). With the widespread loss of sagebrush habitat, threats to

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remaining habitat (Davies et al., 2011), and the subsequent decline of sagebrush-obligate wildlife species (Connelly et al., 2000; Crawford et al., 2004), waiting several decades to over a century for sagebrush recovery will likely not meet management goals.

However, the success of sagebrush restoration efforts has been highly variable. In Idaho, 23 out of 35 areas seeded with Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) had no recruitment of sagebrush (Lysne and Pellant, 2004). Sagebrush density and cover on the remaining seeded areas were low and not different from the unseeded areas (Lysne and Pellant, 2004). In contrast, broadcast-seeding sagebrush after fires in conifer-encroached mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) communities has often been successful at reestablishing sagebrush densities similar to intact communities (Davies et al., 2014; Davies and Bates, 2017). Success, however, was limited on steep south slopes (Davies and Bates, 2017) and when seeded 4 yr after fire because of greater competition from herbaceous vegetation (Davies et al., in press). Increasing the probability of successfully establishing big sagebrush from seed is needed, particularly in lower-elevation sagebrush communities.

Seed pillows (Madsen and Svejcar, 2016), a seed enhancement technology, may be a method to improve the success of broadcast-seeded sagebrush. Seed pillows are a square (pillow-shaped) agglomeration of absorbent materials and other beneficial additives with seeds incorporated within (Madsen and Svejcar, 2016). With precipitation, the seed pillows are designed to break down over the seed, providing seed coverage and enhanced conditions for establishment and growth (Madsen et al., 2016). In a greenhouse experiment, seed pillows improved bunchgrass growth 3.9–5.1 times compared with nontreated seeds (Madsen et al., 2013). In another greenhouse study, Wyoming big sagebrush seedling emergence was 22-fold greater with seed pillows than nontreated seeds (Madsen unpublished data). However, before seed pillows can be recommended for restoration of sagebrush, they require thorough field evaluations across a broad range of site conditions.

The purpose of this study was to evaluate the use of seed pillows for restoring Wyoming and mountain big sagebrush across a large elevation gradient on sites burned in the Long Draw and Holloway wildfires in 2012. To accomplish this objective, we compared broadcast-seeding sagebrush seed incorporated into seed pillows with bare seed. Our hypotheses were that 1) sagebrush cover, density, height, and volume would be greater with the seed pillows compared with the bare seed treatment; and 2) that the benefit of the seed pillows would increase with decreasing elevation.

Methods

Study Area

The study area was located in southeastern Oregon within the Holloway and Long Draw Wildfires. These wildfires burned approximately 412 163 ha (~1 million ac) in 2012. Elevations of the study sites ranged from 1 219 to > 2 134 m above sea level. Before burning, plant communities were primarily Wyoming big sagebrush and mountain big sagebrush communities, with Wyoming big sagebrush transitioning to mountain big sagebrush with increasing elevation. Site characteristics such as plant community composition, precipitation, slope, aspect, and soils varied across the study sites. Climate is typical for the northern Great Basin, with hot summers, cool winters, and most precipitation occurring in the winter and spring. Average long-term (30-yr) annual precipitation ranged from 212 to 593 mm across the study sites (PRISM, 2017). In 2014, annual precipitation ranged from 98% to 110% of the long-term average. However, May and June precipitation in 2014 was 29–35% of the long-term average. In 2015, annual precipitation averaged 84–127% of the long-term average, with percent of average decreasing with increasing elevation. May precipitation in 2015 averaged 220% and 212% of the long-term average at the two lowest elevations (1 219 and 1 372 m). In 2016, annual precipitation ranged from 81–96% of the long-term average.

Experimental Design and Measurements

We evaluated fall broadcast-seeding seed pillows compared with bare seed in 2013 and 2014 (1 and 2 yr post wildfire) at 35 sites in the Holloway and Long Draw Wildfires across an elevation gradient (1 219 to > 2 134 m) using a complete block design. Each year, treatments were replicated five times at seven elevations (approximately 1 219, 1 372, 1 524, 1 676, 1 829, 1 981, and 2 134 m). The total number of plots was 140 (5 replications × 7 elevations × 2 yr × 2 treatments = 140 plots). Elevation replicates were spread widely across the burned landscape and varied in aspect and slope. At each replication, treatments were randomly applied to 5 × 10 m plots at a rate of 1 000 pure live sagebrush seeds·m^{-2} in October of each seeding year. Treatment plots were separated by a 2-m buffer. Pure live seed was estimated using the petri dish germination method (Meyer and Monsen, 1991). Mountain and Wyoming big sagebrush seed was provided by the Utah Division of Wildlife Resources Great Basin Research Center (Ephraim, Utah). Wyoming and mountain big sagebrush was seeded from 1 219 to 1 524 m and 1 676 to 2 134 m, respectively.

Seed pillows were made by thoroughly mixing dry materials (super absorbent polymers, binders, and other beneficial additives including compost and worm castings) and then mixing with liquid ingredients (water, surfactant, and plant growth regulator) to form a dough (Madsen and Svejcar, 2016). The dough material was passed through an industrial dough extruder (Moline Machinery LLC, Duluth, Minnesota) that had a rectangular 8 × 16 mm–wide die. Extruded material was then cut into 16-mm lengths creating seed pillows that were 8-mm thick and 16-mm wide × 16-mm long. Seed pillows were forced-air dried and stored in a cool storage area until seeded.

Vegetation measurements were conducted in late June and early July in 2014, 2015, and 2016. Sagebrush and other shrub density were measured by counting all plants rooted inside the 5 × 10 m plot. Sagebrush height and two perpendicular crown widths were measured on 10 (except when plot density was < 10 sagebrush plants) randomly selected sagebrush plants per plot. Volume was determined from the height and perpendicular crown widths. Average sagebrush volume was multiplied by sagebrush density to determine volume per unit area ($cm^3 \cdot m^{-1}$). Transects were placed at 1.5-m, 2.5-m, and 3.5-m locations along the 5-m side of the treatment plot. Herbaceous vegetation cover and density were measured in nine 0.2-m^2 quadrats in each treatment plot; the quadrats were placed along each of the 10-m transects at the 3-m, 5-m, and 7-m marks. Herbaceous canopy cover was visually estimated by species in the 0.2-m^2 quadrats. Additionally, cover of bare ground, litter, rock, and basal area of vegetation were also estimated in each quadrat. Species density was measured by counting all plants rooted inside the 0.2-m^2 quadrats. We considered a seeding successful if the average sagebrush density was ≥ 0.25 plants·m^{-2} across the five sites at that elevation for that seeding year.

Statistical Analyses

Repeated measure analysis of variance (ANOVA) was used to compare sagebrush cover and density and other vegetation responses that were repeatedly measured between treatments using the PROC MIXED method in SAS 9.4 (SAS Institute, Inc., Cary, North Carolina). Other vegetation was partitioned into groups for analyses: Sandberg bluegrass (*Poa secunda* J. Presl), large perennial grasses, perennial forbs, annual grasses, annual forbs, and other shrubs. Sandberg bluegrass was treated as a separate group from other perennial grasses because it responds differently to disturbance and matures earlier in the growing season. The other shrub group comprised shrubs excluding sagebrush. Each seeding year was analyzed individually because of differing number of sampling years (3 yr and 2 yr for the first and second seedings, respectively). Sampling year was the repeated variable, and treatment was considered a fixed variable in models. Explanatory variables were elevation, sampling year, elevation · treatment interaction, and treatment · sampling year interaction. Compound symmetry was selected as the appropriate covariance structure using Akaike's Information Criterion (Littell et al., 1996). Final sagebrush height and volume in 2016 was compared between treatments with an ANOVA using a mixed model in SAS 9.4. Explanatory variables were treatment, elevation, seeding year, elevation · treatment interaction, and treatment · seeding year interaction. Data that violated assumptions of ANOVAs were square root transformed to better meet assumptions. Original (i.e., nontransformed) data were presented in the text and figures. Means were considered different at $P \le 0.05$ and were reported with standard errors.

Results

Sagebrush density did not differ between the seed pillow and bare seed treatments seeded in 2013 and 2014 (Fig. 1A and B; $P = 0.917$ and 0.120). Sagebrush density varied by elevation in both the 2013 and 2014 seedings (see Fig. 1A and B; $P < 0.001$ and < 0.001). Sagebrush density in the 2013 seeding was greatest at the higher elevations. In contrast, sagebrush density in the 2014 seeding was greatest at the lowest elevation. Sampling year, elevation · treatment interaction, and sampling year · treatment interaction did not influence sagebrush density in either the 2013 or 2014 seedings ($P > 0.05$). Sagebrush cover did not differ between treatments in either seeding year (Fig. 2A and B; $P = 0.990$ and 0.186). Elevation influenced sagebrush cover in the 2013 and 2014 seedings (see Fig. 2A and B; $P < 0.001$ and < 0.001). Sagebrush cover generally increased with elevation in the 2013 seeding. In the 2014 seeding, sagebrush cover was greater in the lowest and highest elevations compared with the midelevations. Sampling year, elevation · treatment interaction, and sampling year · treatment interaction did not influence sagebrush cover in either the 2013 or 2014 seedings ($P > 0.05$). Final year sagebrush height and volume per unit area did not differ between treatments ($P = 0.290$ and 0.782). Sagebrush heights were generally lowest in the middle elevations, with the greatest heights at 2134 m followed by 1219 m elevation (Fig. 3). Sagebrush volume per unit area followed a similar pattern (data not shown). Elevation was the only explanatory variable that influenced sagebrush height and volume ($P < 0.001$ and < 0.001). Other vegetation cover and density, bare ground, litter, and biological soil crusts did not differ between treatments (data not shown; $P > 0.05$).

Sagebrush restoration success (≥ 0.25 sagebrush·m^{-2}) varied by elevation and year (Table 1). Summarized for the 2 seeding yr, both seed pillows and bare seed had a 36% success rate. However, 50% of the sites had either seed pillows, bare seed, or both treatments result in successful restoration. Furthermore, if both seeding methodologies were used in back-to-back years, seeding success would have been 86% (six out of seven elevations).

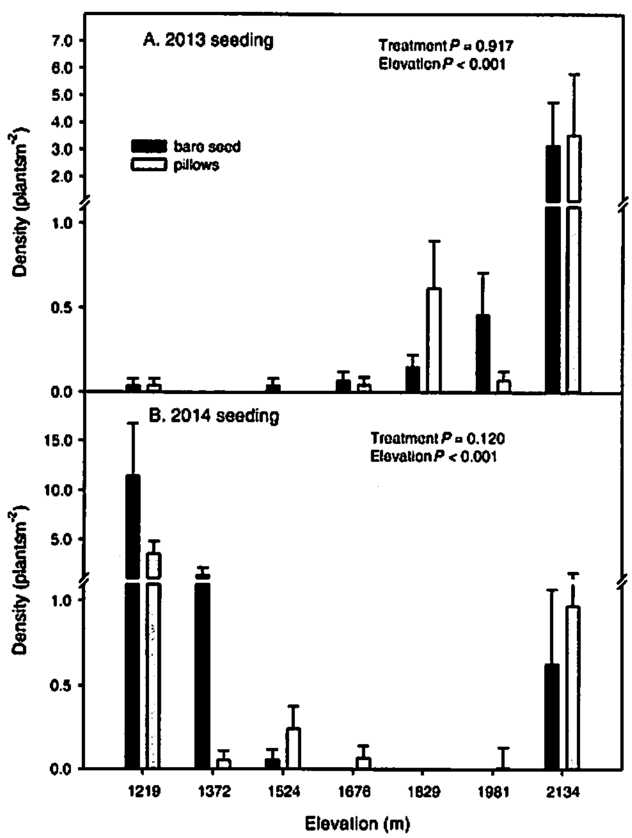

Figure 1. Sagebrush density (mean + S.E.) in bare seed and seed pillow treatments broadcast-seeded in 2013 and 2014 across a large elevation gradient in the northern Great Basin. Data were averaged for 2014, 2015, and 2016 for the 2013 seeding and 2015 and 2016 for the 2014 seeding.

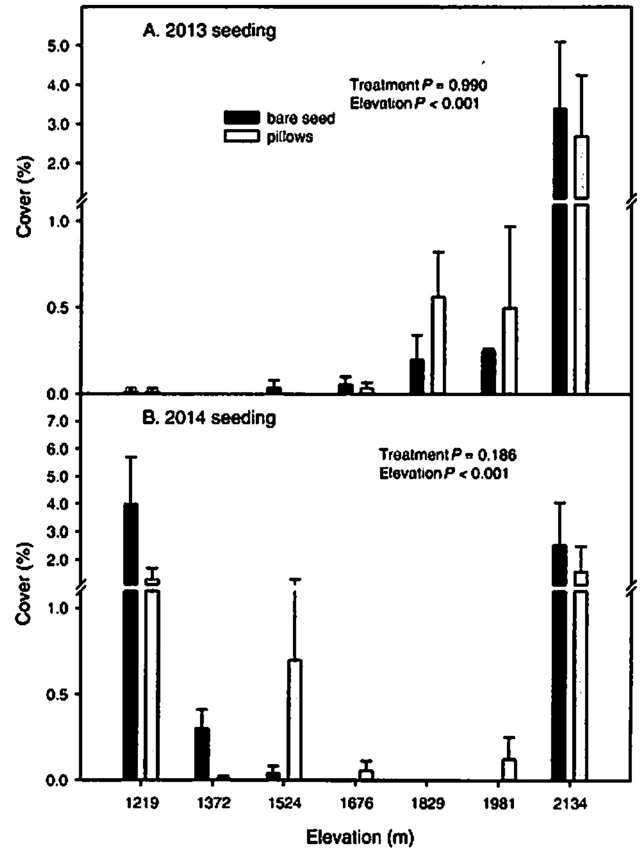

Figure 2. Sagebrush cover (mean + S.E.) in bare seed and seed pillow treatments broadcast-seeded in 2013 and 2014 across a large elevation gradient in the northern Great Basin. Data were averaged for 2014, 2015, and 2016 for the 2013 seeding and 2015 and 2016 for the 2014 seeding.

Discussion

Counter to our hypothesis, broadcast-seeded seed pillows did not improve sagebrush establishment success compared with broadcast-seeded bare seed in either seeding year. Also in contrast to our expectations, the effect of seed pillows compared with bare seed on sagebrush density and cover did not vary by elevation. Sagebrush height and

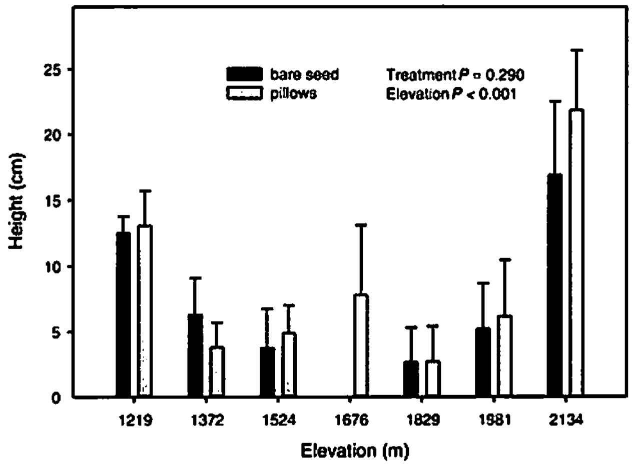

Figure 3. Sagebrush height in bare seed and seed pillow treatments in 2016 across a large elevation gradient in the northern Great Basin. Data were summarized for the 2013 and 2014 broadcast seedings.

volume were also similar between seed pillow and bare seed treatments. Therefore, we conclude that the seed pillow formulation used in our study was not advantageous compared with less expensive bare seed for restoring big sagebrush after wildfires in the northern Great Basin. In previous greenhouse studies, seed pillows improved bunchgrass seedling growth (Madsen et al., 2013) and sagebrush emergence (Madsen unpublished data). Differences between our results and greenhouse studies (Madsen et al., 2013; Madsen unpublished data) are likely linked to the substantial environmental variability between field conditions and greenhouse experiments. Greenhouse experiments generally limit the amount of stress that seedlings experience. Comparatively, in sagebrush steppe environments, temperatures fluctuate widely, precipitation can be erratic, and periodic drought is common. This highlights the importance of validating greenhouse results with field experiments over multiple years.

We speculate that broadcasted seed pillows were not an improvement on bare seed because seed-soil contact was not enhanced. In the field, we observed that the super-absorbent materials swelled with water following a precipitation event, but as the seed pillows dried, they often disconnected from the soil surface, reducing the likelihood that the radicle could penetrate the soil surface quick enough to stay ahead of the soil drying-front. Broadcasted seed pillows also did not appear to break down in the field as rapidly as we had anticipated. The shrinking and swelling of absorbent materials may have also contributed to seedling mortality by damaging the seedling radicle. These were not issues in the greenhouse, where watering and environmental conditions were held more constant. Broadcasted seed pillows could possibly improve sagebrush establishment if they broke down more rapidly, covered the seed, and stayed connected to the soil surface. We suggest that super-absorbent materials be used with caution in seed pillows that will be broadcast seeded.

Though seed pillows were not advantageous compared with bare seed, they were considered successful (≥ 0.25 sagebrush·m^{-2}) at some elevations in at least 1 of the 2 seeding yr when bare seed was not and vice versa (see Table 1). Pillows and bare seed each had a success rate of 36%; however, if we only required that one of the two methods be successful, sagebrush restoration was successful on 50% of the seedings. Thus, sagebrush restoration success could have been improved by seeding both bare seed and seed pillows. Seeding both could be considered a form of bet hedging to improve the odds that some sagebrush would be established compared with only seeding one of the two treatments. Further supporting the concept of using bet hedging, we found that if we had seeded in 2 yr combined with two seeding methods, then our success rate would have been 86%. This suggests that incorporating a seed technology to delay germination in some of the seeds for a year may improve the odds of having seeds available when conditions are conducive for establishment. Bet hedging seeding may be important because conditions for successful establishment are sporadic, often varying spatially and temporally in rangelands. Our success rates may also have been greater if we had been able to seed immediately after the fire (Evans and Young, 1978). Allowing herbaceous vegetation to recover after fire before seeding sagebrush may decrease the likelihood of establishing sagebrush because of increased competition (Davies et al., in press).

Elevation was an important factor influencing sagebrush survival and growth. However, elevation effect was not always intuitive, particularly in the second-yr seeding. In the first-yr seeding, sagebrush density and cover generally increased with elevation. This was expected because increasing elevation results in cooler, moister growing conditions that likely favor establishment of seeded species in the sagebrush steppe ecosystem (Davies et al., 2011). However, in the second-yr seeding, sagebrush cover and density were greatest in the lower elevations and the highest elevation. The greater sagebrush cover and density at the highest elevation was expected, as conditions are generally more favorable for sagebrush seedlings. Greater sagebrush cover and density in the lower elevations probably occurred because little vegetation existed in these areas after 2 postwildfire years of spring drought and then, in the third spring after fire, precipitation greatly exceeded the long-term average (Fig. 4). Thus, in the second seeding, competition from herbaceous vegetation was minimal in the lower elevations when a wet spring occurred. In the third yr after fire, spring precipitation and annual precipitation as a percent of the long-term average generally decreased with increasing elevation across the study area (PRISM, 2017). Thus, at midelevations, competition from herbaceous vegetation may have limited sagebrush establishment in an average to below-average precipitation year. Competition from herbaceous vegetation can limit sagebrush and other shrub establishment (Schuman et al., 1998; Rinella et al., 2015, 2016; Davies et al., in press) and, thus, should be considered when planning sagebrush restoration. Competition from herbaceous vegetation may require that herbaceous vegetation be reduced to restore sagebrush (Boyd and Svejcar, 2011). Results from our study suggest that there is an interesting interaction between multiyear precipitation and competition that can greatly influence the success of sagebrush restoration, even producing results that are counter to the general assumption that sagebrush establishment and growth increase with increasing elevation.

Implications

The seed pillow formulation evaluated in this study did not convey any benefits in establishment or growth of sagebrush over bare seed

Table 1
Sagebrush restoration success using seed pillows and bare seed broadcast-seeded in 2 yr across an elevation gradient in southeast Oregon. Seedings were considered successful if sagebrush density was ≥ 0.25 plants·m^{-2} averaged across the 5 sites at that elevation. The "Combined" category was considered successful if at least 1 of the methods was successful in at least 1 of the seeding yr at that elevation

Seeding	Elevation (m)						
yr	1219	1372	1524	1676	1829	1981	2134
2013	Both fail	Both fail	Both fail	Both fail	Pillows successful	Bare successful	Both successful
2014	Both successful	Bare successful	Pillows successful	Both fail	Both fail	Both fail	Both successful
Combined	Success	Success	Success	Fail	Success	Success	Success

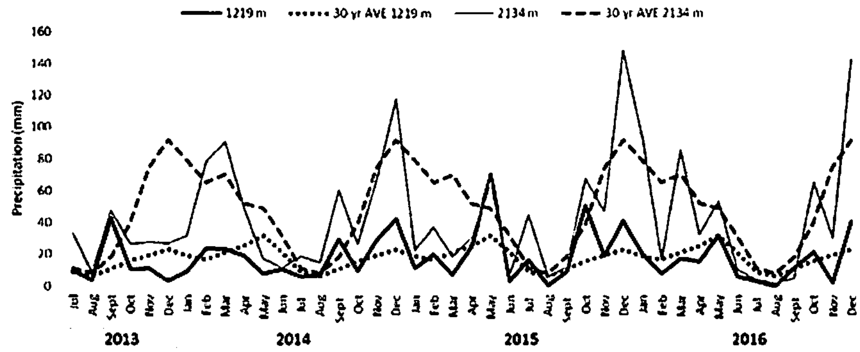

Figure 4. Monthly precipitation during the study and 30-yr average (AVE) at 1 219 m and 2 134 m study sites (PRISM, 2017).

across the entire elevation gradient. This, combined with the added expense of seed pillows, strongly suggests that when only one method will be used, broadcast seeding of bare seed is a better option for restoring sagebrush after wildfire than broadcasting seed pillows. Seed pillows may be improved by redesigning them, but any new design will need to be thoroughly tested. Alternatively, we suggest that the best method for restoring sagebrush may be to seed both bare seed and seed pillows because the pillows were successful at times that bare seeds were not and vice versa. Seeded individually, both seed pillows and bare seed had a 36% success rate. However, the success rate increased to 50% if only one of the methods needed to be successful. Seed enhancement technologies (seed coating, pillows, etc.) have the potential to increase restoration success (Madsen et al., 2016); however, they must overcome the most limiting factor(s) to seedling establishment in the field, which vary temporally and spatially. Thus, one method is unlikely to be the best method at every location in every year. Bet hedging, seeding bare seed and seeds with varying seed enhancement technologies, may increase the probability that at any given location, some seeded species will establish because limiting factors will be mediated for at least a portion of the seeds and that some seeds will likely germinate when conditions are conducive for establishment.

Our research also demonstrated that elevation is a critical factor in determining restoration success. However, success was not as straightforward as expected since it did not necessarily increase with elevation. Multiyear precipitation likely has a significant interaction with elevation effect on sagebrush seedling establishment. Thus, lower elevations cannot necessarily be assumed to be unrestorable, nor is increasing elevation always positively correlated to increasing establishment of seeded species in the Great Basin.

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