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Influence of Aboveground Vegetation on Seed Bank Composition and Distribution in a Great Basin Desert Sagebrush Community

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1 **Influence of aboveground vegetation on seed bank composition and distribution in a**
2 **Great Basin Desert sagebrush community**

3

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16   **Abstract**

17
18   The quantity, composition, and spatial dispersion of seed banks can greatly affect

19   community dynamics. While seed banks of hot deserts have been studied extensively, little is

20   known about seed banks in cold deserts, in particular the relationship between the seed bank and

21   the aboveground vegetation. We investigated the relationship between the seed bank and

22   aboveground vegetation and the effect of microhabitat (shrub interspace or beneath shrub) and

23   aboveground community phase (high or low perennial bunchgrass cover) on the seed bank of a

24   Great Basin Desert sagebrush community. The seed bank and aboveground vegetation differed

25   in their most dominant species, resulting in moderately dissimilar species compositions as

26   determined by Sørensen's similarity index and Bray-Curtis distance. In contrast, comparing the

27   seed bank species composition to the aboveground vegetation structure (functional groups) using

28   non-metric multidimensional scaling (NMDS) revealed a correspondence between the two

29   communities. Shrub seed densities were higher beneath shrubs. Neither microhabitat nor

30   community phase explained variation in total seed density or species richness. Therefore, our

31   measures of the aboveground vegetation did not influence seed density across functional groups

32   or species richness, and the similarity between the seed bank and aboveground vegetation varied

33   depending on the aboveground organizational level used in comparisons.

34   Key words: seed bank, aboveground vegetation, shrub, Great Basin Desert, similarity,

35   microhabitat

36
37   **1. Introduction**
38
39   The majority of Great Basin Desert species rely on seeds for propagation; however, seed

40   banks (or seed pools)of this desert are poorly understood (Kemp, 1989). Seed banks may help

41   re-establish species that have become locally extinct aboveground. Evaluations of North

42   American desert seed banks suggest that those of the Great Basin Desert consist of fewer annual

43   and more perennial species than do hot desert seed banks (Kemp, 1989; Guo et al., 1999).

44   Although maximum seed densities are generally similar among the North American deserts,

45   there are some areas of the Great Basin Desert that appear to have very small seed banks (Hassan

46   and West, 1986).

47   Annual species are more likely than perennial species to form persistent seed banks

48   because they tend to produce dormant seeds (Jurado and Flores, 2005). This strategy allows

49   seeds to wait for proper germination cues which may increase the chance of establishment and

50   survival. However, a long-term seed banking strategy may be difficult for annuals to achieve

51   because of seed reductions caused by continuous germination and granivory (Kigel, 1995). Due

52   to the nature of perennial species, seeds are less likely to be dormant, and therefore, seed banks

53   tend to be transient. Species that form transient seed banks are at risk of becoming locally

54   extinct, especially if seed production is limited (O'Connor, 1991). Seed production can be

55   limited by a number of factors, such as invasive species which may cause native perennial

56   species to produce fewer seeds and die prematurely if the density of the invader is high (Vilà and

57   Gimeno, 2007) or by drought years that limit flowering and seed production (St. Clair et al.,

58   2009).

59   The invasion of *Bromus tectorum* (cheatgrass) has altered the structure and composition

60   of Great Basin Desert seed banks. Studies examining seed banks of degraded sagebrush

61   communities have shown shifts to greater annual seed abundance with cheatgrass invasion

62   (Young and Evans, 1975; Humphrey and Schupp, 2001). Even in systems that are not

63   considered to be dominated by cheatgrass, introduced species can still account for 20 percent of

64   the total number of seeds in the seed bank (Guo et al., 1999).

65   The relationship between the seed bank and aboveground vegetation is not well

66   understood in Great Basin Desert sagebrush communities. Plant communities dominated by

67   perennial species usually have relatively low aboveground-belowground similarities, while

68   annual-dominated communities tend to have a greater correspondence between aboveground

69   vegetation and the seed bank (Thompson and Grime, 1979; Ungar and Woodell, 1993; Milberg,

70   1995; Bakker et al., 1996; Osem et al., 2006), at least partly because annual-dominated

71   communities arise yearly from the available seed bank, which reflects vegetation of the previous

72   year (Osem et al., 2006).

73   When comparing the relationship between the seed bank and aboveground vegetation

74   among forest, grassland (including desert), and wetland seed banks, grassland standing

75   vegetation is most similar to the seed banks in terms of species composition (Hopfensperger,

76   2007). In desert grasslands, extreme environmental conditions may select for species that rely on

77   persistent seed banks, resulting in similar above and belowground communities (Henderson et

78   al., 1988). However, higher similarity between the seed bank and aboveground vegetation in

79   desert grasslands is more likely due to limited dispersal and aggregated seed patterns

80   surrounding parent plants (Shaukat and Siddiqui, 2004). In contrast, some studies have found a

81   lack of correspondence between the seed bank and aboveground vegetation in grasslands which

82   has been attributed to different dominant species in the aboveground and seed bank communities

83   (Eriksson and Eriksson, 1997; Kalamees and Zobel, 1997). For example, the most dominant

84   species in the seed bank may be overrepresented due to high production of small seeds (Eriksson

85   and Eriksson, 1997).

86   The aboveground vegetation not only influences the community composition of the seed

87   bank but also the distribution of the seeds. Although the distribution of seeds within desert seed

88   banks is spatially variable, seeds are frequently more abundant under shrub and tree canopies

89   than in interspaces (Nelson and Chew, 1977; Guo et al., 1998; Marone et al., 2004) and exhibit

90   an aggregated seed pattern due to seeds settling close to the mother plant (Shaukat and Siddiqui,

91   2004). A study investigating spatial patterns of species richness found higher species richness at

92   the mid-point and furthest sampling point from shrubs (2 m and 6 m from shrubs ; Li, 2008). In

93   pinyon-juniper woodlands, seed densities and species richness were highest in interspaces and

94   the interface between interspaces and litter under trees (Koniak and Everett, 1983). Shrubs and

95   trees affect the spatial distribution of seeds as they can act as a barrier, altering wind dynamics

96   and subsequent seed deposition patterns. (Guo et al., 1998; Li, 2008; Li et al., 2009). Seeds

97   often accumulate beneath shrubs because they decrease wind velocity and physically trap seeds,

98   leading to deposition close to shrubs (Bullock and Moy, 2004). Seeds can also be redistributed

99   from interspaces to litter beneath shrubs by wind and water (phase II dispersal; Chambers and

100 MacMahon, 1994).

101   This study explores the seed bank and the aboveground vegetation within a Great Basin

102 Desert plant community and how the aboveground vegetation influences the seed bank

103 community composition and seed distributions. Specific goals were to determine the

104 relationship between the compositions of the seed bank and the aboveground vegetation and the

105 effect of shrubs (microhabitat effects) and perennial bunchgrass cover (community phase effects)

106 on the seed bank community composition, seed density, and seed bank species richness.

107
108 **2. Methods**
109
110
111 *2.1. Study site*

112   Soil seed bank samples were collected from the Onaqui Sagebrush/Cheatgrass SageSTEP

113   research site in Tooele County, Utah, USA, about 40 km south of Tooele, UT (40°11'53"N

114   112°27'51"W). The Onaqui site is located on the eastern toeslope of the Onaqui mountains at an

115   elevation of 1750-1850 meters (McIver et al., 2010).   Based on Utah Climate Center data from

116   the Vernon climate station (Latitude: 40.1125, Longitude: -112.435; Elevation: 1671 m; Period:

117   1953-2010), about 11.3 km south of the study site and in the same valley, mean monthly

118   temperature ranges from -3.1 C in January to 22.0 C in July, while mean monthly precipitation

119   ranges from 17.5 mm in December to 29.5 mm in May, yielding a mean annual precipitation of

120   264.4 mm. Snow can occur in all months except July and August with a peak in January (Utah

121   Climate Center, 2012). Onaqui has fine-loamy soils (McIver et al., 2010).

122   Characteristic vegetation of this site includes Wyoming big sagebrush (*Artemisia*

123   *tridentata* ssp. *wyomingensis*), shadscale saltbush (*Atriplex confertifolia*), yellow rabbitbrush

124   (*Chrysothamnus viscidiflorus*), Sandberg bluegrass (*Poa secunda*), squirreltail (*Elymus*

125   *elymoides*), Indian ricegrass (*Achnatherum hymenoides*), bluebunch wheatgrass

126   (*Pseudoroegneria spicata*), basin wildrye (*Leymus cinereus*), and cheatgrass (*Bromus tectorum*).

127   Seed bank germination assays were conducted at the Utah State University Research

128   Greenhouse Facility in Logan, UT.

129
130   *2.2. Experimental design*

131   This study presents the results of baseline sampling of the seed bank of the Onaqui

132   sagebrush-cheatgrass site of the SageSTEP network (McIver et al., 2010). The sagebrush-

133   cheatgrass portion of SageSTEP is a large experimental study addressing the effects of

134   restoration treatments (control, prescribed burn, mow, tebuthiuron herbicide, and imazapic

135   [Plateau®] pre-emergent herbicide) on sagebrush ecosystems. Burn, mow, and tebuthiuron

136   treatments were designed to reduce shrub cover, while imazapic is used to reduce the emergence

137   and establishment of exotic annuals. All results presented in this paper are pretreatment and thus

138   do not address the effects of treatments; nonetheless, we describe the experimental design and

139   refer to sampled plots and subplots by their treatment names because treatment effects will be

140   addressed in a subsequent paper. In the present study, the treatment plots should be viewed

141   simply as replicate plots of untreated sagebrush ecosystems.

142   Control, prescribed burn, mow, and tebuthiuron treatments were applied at the whole plot

143   level (75 acres; 30.4 ha), while imazapic was applied at the subplot level (0.1 ha) as a split-plot

144   factor in all whole plots. In the seed bank studies at Onaqui the mow treatment was excluded,

145   leaving three plot-level treatments and one subplot-level treatment.

146   In each sampled plot, subplots with two levels of perennial bunchgrass cover were

147   sampled. Community phases were chosen by dividing the cover of perennial bunchgrasses into 3

148   ranges. Subplots with greater than 19 percent perennial bunchgrass cover were considered phase

149   1 communities, those with 10-19 percent bunchgrass cover were considered phase 2, and those

150   with less than 10 percent perennial bunchgrass cover were considered phase 3 communities. In

151   the present study only phase 1 and 3 communities were sampled in order to examine the effects

152   of high and low native bunchgrass covers on seed banks. Four phase 1 subplots and four phase 3

153   subplots that did not receive Plateau[®] were sampled in the control (CO), prescribed burn (FI),

154   and tebuthiuron (TE) plots, and four phase 1 subplots and four phase 3 subplots that did receive

155   Plateau[®] also were sampled in the control plot for a total of 32 subplots. Although the set of the

156   control subplots that received Plateau are not from a true plot, we refer to these subplots as the

157   control-Plateau[®] plot (CP) for convenience.

158
159   *2.3. Seed bank sampling*

160

161   Soil seed bank samples were collected 14-17 and 22-24 August 2006. Within each 0.1-ha

162   (30 x 33 m) subplot, four 28-m transects were laid out so as to not interfere with vegetation

163   surveys. Transects ran north-south and were located at 3, 10, 20, and 27 meters from the

164   northwest corner of the subplot. A composite sample consisting of 5 subsamples from within a

165   25 x 25-cm frame was collected every 3 meters along each of the 4 transects for a total of 10

166   composite samples per transect and 40 per subplot. Collecting many small samples has been

167   shown to increase the precision of estimates of seed numbers in the soil (Bigwood and Inouye,

168   1988). If necessary, sampling locations were shifted slightly in order to assure that all 5

169   subsamples were from the same microhabitat (see below). Subsamples measured 6.1 cm in

170   diameter and were taken to a depth of 4 cm with PVC couplings. Litter and soil layers were

171   collected together. Microhabitat (shrub interspace or beneath shrub) was recorded for each

172   composite sample collected.

173
174   *2.4. Vegetation surveys*

175   Aboveground vegetation surveys were conducted on transects located at 2, 7, 15, 23, and

176   28 meters from the northwest corner of each subplot. The line-point intercept method was used

177   to measure the cover of each species present along each transect (Herrick et al., 2005). Species

178   intercepted by the pin were recorded every half meter totaling 60 points per transect and 300

179   points per subplot. Subplots were then surveyed to account for any additional species that were

180   not encountered on transects and were assigned a dominance class. Class 1 represents rare

181   species (1-2 plants per subplot); class 2 represents sparse species (<5% cover); class 3 represents

182   common species (5-25% cover); class 4 represents co-dominant species (25-50% cover), and

183   class 5 represents dominant species (>50% cover). Of the additional species found in the subplot

184 survey, none had a higher dominance than 3. Dominance classes were then converted to relative

185 abundance for analysis. Class 1 was converted to 0.0033 (equivalent to a species being hit once

186 during line-point intercept). Class 2 was converted to 0.04 (4% cover), and class 3 was

187 converted to 0.15 (15% cover). Vegetation surveys were conducted in summer 2006.

188 Nomenclature for all plant species followed the USDA NRCS PLANTS Database (2009).

189
190 *2.5. Evaluating the seed bank*
191
192   The germinable seed bank was evaluated by direct germination in a greenhouse following

193 cold-moist stratification, which has been shown to be an efficient and reliable method for

194 determining species presence in the germinable seed bank (Gross, 1990).   Each composite

195 sample was moistened to field capacity and kept in an unlighted refrigerator at 2°C. After 60

196 days of stratification, samples were removed from the refrigerator and spread over a 2-cm layer

197 of sand in planting trays with drainage holes. Planting trays were divided into three 25.4 X 16.9-

198 cm compartments, each containing one soil sample. Spread out soil samples had a depth of ≈1.3

199 cm and a volume of ≈585 cm^3. Samples were kept moist, and seedlings were identified, counted,

200 and removed as they emerged. Individuals that were not identified in the seedling stage were

201 transplanted and grown until mature.

202   Due to the high volume of samples collected, not all seed bank samples were evaluated at

203 the same time. Therefore, depending on the availability of greenhouse space, varying numbers

204 of samples were randomly selected from each treatment combination for each germination assay.

205 Eleven of the 40 samples from each treatment combination were germinated and evaluated for

206 each of the first and second germination assay. Six samples from each treatment combination

207 were germinated and evaluated for the third germination assay, and nine samples were

208 germinated and evaluated for the fourth germination assay. Thus, a total of 37 of the 40 samples

209   per subplot were germinated. Each germination assay lasted 150 days. Emergence was initially

210   censused for 115 days, at which point emergence was noticeably reduced. Samples were then

211   dried out for 14 days and mixed, after which watering was resumed and emergence was censused

212   for an additional 21 days.

213   The first germination assay ran from mid-January to mid-June 2007. The second

214   germination assay ran from mid-June to mid-November 2007. The third germination assay ran

215   from mid-January to mid-June 2008, and the fourth germination assay ran from mid-June to mid-

216   November 2008. First and third germination assays and second and fourth assays ran during the

217   same time of year so as to control for potential seasonal germination effects that could bias

218   results.

219
220   *2.6. Statistical Analysis*
221
222   Sørensen's similarity index (C_s) and Bray-Curtis distance (BC) were calculated in R

223   version 2.6.2 (R Development Core Team, 2008) to compare the seed community to the

224   aboveground community. These two similarity/distance metrics compare two communities in

225   different ways. Sørensen's similarity is based strictly on presence/absence: $C_s=2w/(2w+A+B)$

226   where w is the total number of species found in both communities, A is the number of species

227   excusive to aboveground, and B is the number of species exclusive to belowground. A C_s of 0

228   represents completely dissimilar communities and C_s of 1 represents identical communities at the

229   level of presence/absence. In contrast to Sørensen's similarity index, Bray-Curtis distance

230   incorporates information on relative abundance (or cover). This metric normalizes relative

231   abundance for communities being compared by dividing the absolute differences by the

232   summation: $BC = \sum_{i}^{n} | x_{ij} - x_{ik} | / \sum_{i}^{n} x_{ij} + x_{ik}$ where x_{ij} is the relative abundance of species i in

233   community j, x_{ik} is the relative abundance of species i in community k, and n is the total number

234   of species. A BC of 0 represents most similar communities, and a BC of 1 represents most

235   different communities. C_s and BC were calculated for the entire site and for each plot using

236   relative cover of the aboveground community and relative abundance of the germinable seed

237   bank community to avoid differences in sampling scales.

238   To further compare the community composition of the germinable seed bank to that of

239   the aboveground vegetation, seed bank composition data were ordinated by non-metric

240   multidimensional scaling (NMDS) with a Bray-Curtis distance measure using the metaMDS

241   function in the Vegan package in R version 2.11.1 (Oksanen et al., 2008; R Development Core

242   Team, 2008). Specifically, seed bank composition was compared to the aboveground vegetation

243   structure by assigning one of seven functional groups to all species present aboveground: annual

244   forbs, annual grasses, perennial forbs, perennial grasses, *Poa secunda*, shrubs, and trees. As with

245   the similarity and distance metrics, relative cover of the aboveground community and relative

246   abundance of the germinable seed bank community were used to avoid differences in sampling

247   scales. Functional groups were based on different morphologies and root systems. *Poa secunda*

248   was considered a different functional group than perennial grasses because *P. secunda* is a

249   shorter grass that has a shallower root system compared to the other perennial grasses. The

250   relative covers of aboveground functional groups were fitted and plotted onto the seed bank

251   species composition ordination solution using the envfit function in the Vegan package in R

252   version 2.11.1 with $P < 0.05$ to determine significance (Oksanen et al., 2008; R Development

253   Core Team, 2008). NMDS on densities of germinable seed bank species was also used to

254   compare beneath shrub (S) and shrub interspace (I) community compositions and to compare

255   phase 1 and phase 3 community compositions.

256   To determine the number of dimensions for each NMDS, stress values were assessed.

257   Stress is a measure of how much the distances in the reduced ordination space depart from the

258   distances in the original p-dimensional space. High stress values indicate a possibility that sites

259   are randomly being placed without any relation to the original distances. Therefore, ordinations

260   with the lowest possible stress are desirable; values up to 20 are acceptable and can be

261   interpreted ecologically (Clarke, 1993). Regardless of the number of dimensions chosen, all

262   figures are shown in two dimensions because the third dimension did not seem to alter results

263   upon inspection.

264   A mixed-model factorial ANOVA (analysis of variance) was performed to detect

265   differences in total seed density and species richness (total number of species present) between

266   aboveground microhabitat and community phase using the MIXED procedure in SAS version

267   9.1.3 (SAS Institute, 2003) and $P < 0.05$ to determine significance. Microhabitat and community

268   phase were treated as fixed effects, and plot and subplot were random effects. Because seed

269   bank species composition data were sparse and did not meet the assumptions of normality and

270   heteroscedasticity, seed bank species were grouped into functional groups and analyzed to

271   understand how aboveground microhabitat and community phase affect the structure of the seed

272   bank community. The same ANOVA model described above was used to detect seed density

273   differences within each of six functional groups: annual forb, annual grass, perennial forb,

274   perennial grass, *Poa secunda*, and shrub. One tree species (*Tamarix ramosissima*) was found in

275   the germinable seed bank but was not analyzed as a functional group due to very low seed

276   densities and only one species present. Species richness was not analyzed within functional

277   group because sample sizes were too low and assumptions of normality and heteroscedasticity

278   were unable to be met.

279   Total seed density and species richness across functional groups were log transformed to

280   meet the assumptions of normality and homogeneity of variance. Seed densities within the

281   perennial grass, perennial forb, annual forb, *Poa secunda*, and shrub functional groups were

282   square root transformed. Seed density within the annual grass functional group was log

283   transformed. For significant main effects, least squared means were compared using Tukey's

284   test. Least squared means and standard errors were back-transformed for figures.

285
286   **3. Results**
287
288
289   *3.1. Relationship between the germinable seed bank and aboveground vegetation*
290
291   A total of 47 species germinated from the seed bank, and 43 species were recorded

292   aboveground (Appendix A; Appendix B). The germinable seed bank and aboveground

293   vegetation were moderately different in terms of species presence at the overall site scale

294   according to Sørensen's similarity index (C_s = 0.447). Results were similar for all individual

295   plots (CO C_s = 0.421; FI C_s = 0.436; TE C_s = 0.511; CP C_s = 0.433). When relative abundance

296   was incorporated, Bray-Curtis distance showed a similar trend, where the germinable seed bank

297   and aboveground vegetation were moderately dissimilar at the overall site level and the

298   individual plot levels (Site BC = 0.609; CO BC=0.580; FI BC = 0.587; TE BC = 0.627; CP BC =

299   0.638). Sørensen's similarity index concluded that the CO plot had the most dissimilar

300   aboveground-belowground communities while Bray-Curtis distance found that CP had the

301   highest dissimilarity. According to Sørensen's similarity index the aboveground-belowground

302   communities were most similar in the TE plot. However, Bray-Curtis distance identified the CO

303   plot as having the most similar aboveground-belowground communities.

304   The NMDS with two dimensions was an acceptable representation of the original

305   germinable seed bank data (stress = 7.18). Four of the seven aboveground structure variables

306   (functional groups) were significantly correlated with the germinable seed bank community, with

307   correlations being highly significant for annual grasses and annual forbs, as expected (Table 1).

308   The two most dominant annual grass species present in the germinable seed bank, *Bromus*

309   *tectorum* (brte) and *Vulpia octoflora* (vuoc), were positively correlated with the cover of the

310   aboveground annual grass functional group (Fig. 1).

311
312   *3.2. Effects of micohabitat and aboveground community phase on germinable seed bank*
313   *community, seed densities, and species richness*
314
315
316   *3.2.1. Germinable seed bank community*
317
318   The NMDS plot constructed to compare microhabitats with three dimensions was an

319   acceptable solution (stress=19.88). Interspace and beneath shrub communities did not display

320   distinct community compositions as indicated by the lack of separation in the ordination plot

321   between the two microhabitats (Fig. 2).

322   The NMDS comparing aboveground community phase required three dimensions to

323   achieve an acceptable stress level of 17.38. There was no obvious separation of phase

324   1 and phase 3 community compositions (Fig. 3).

325
326   *3.2.2. Seed density*
327
328   ANOVA showed that seed density was not significantly affected by microhabitat, phase,

329   or the microhabitat x phase interaction (Table 2). Shrub seed density was the only functional

330   group significantly affected by any of the factors (Table 2). Microhabitat had a significant effect

331   on shrub seed density, with more seeds found beneath shrubs (6.74 ± 3.12) than in interspaces

332   (3.17 ± 4.46).

333

334   *3.2.3. Species richness*

335   ANOVA showed that species richness of the germinable seed bank was not significantly

336 affected by microhabitat, phase, or the microhabitat x phase interaction (Table 2).

337
338 **4. Discussion**
339
340
341   *4.1. Relationship between the germinable seed bank and aboveground vegetation*
342
343   Despite findings that desert grassland germinable seed bank communities may

344 correspond to the aboveground vegetation as a result of limited seed dispersal and clustered

345 seeds surrounding parent plants (Shaukat and Siddiqui, 2004), our results from the similarity and

346 distance metrics did not strongly support this expectation. Both Sørensen's similarity index and

347 Bray-Curtis distance indicate that the germinable seed bank and aboveground community

348 compositions were moderately different at the overall site and individual plot levels. At the plot

349 level, Sørensen's similarity index and Bray-Curtis distance give conflicting results as to which

350 plot had the most and least similar aboveground-belowground communities. This is likely due to

351 Sørensen's similarity index giving greater importance to rare species. The germinable seed bank

352 and aboveground vegetation only shared 19 of the total of 71 species encountered in this study.

353 However, for most species present in both the germinable seed bank and aboveground

354 vegetation, relative abundances were similar except that *Alyssum desertorum* and *Ceratocephala*

355 *testiculata* were vastly over-represented in the germinable seed bank relative to the aboveground

356 vegetation while *Artemisia tridentata* was over-represented in the aboveground vegetation

357 relative to the seed bank (Appendix A; Appendix B).

358   Eriksson and Eriksson (1997) have attributed a lack of correspondence between the

359 germinable seed bank and aboveground vegetation to the fact that the dominant species often

360   differ between the two communities. *A. tridentata* was the most dominant species aboveground

361   at the Onaqui site. Young and Evans (1989) found that no *A. tridentata* seeds germinated from

362   the seed bank when collected before fall when *A. tridentata* seeds mature. In contrast, in the

363   present study germinable *A. tridentata* seeds were found in seed bank samples collected in

364   August, before seed dispersal, but at low densities. Therefore, *A. tridentata* was over-

365   represented aboveground, which decreased the similarity between the germinable seed bank and

366   aboveground vegetation. Conversely, *A. desertorum* and *C. testiculata* were abundant in the

367   germinable seed bank but had lower cover aboveground. Annual species such as *A. desertorum*

368   and *C. testiculata* that produce small abundant seeds generally may be over-represented in the

369   germinable seed bank (Eriksson and Eriksson, 1997). Although many factors potentially

370   contribute to seed traits, in general annuals are expected to invest more resources in seed

371   production and, all else equal, produce smaller seeds relative to perennials (Silvertown and

372   Charlesworth, 2001). Also, being annuals, *A. desertorum* and *C. testiculata* can produce large

373   germinable seed banks and use seed banking as a bet hedging germination strategy (Philippi and

374   Seger, 1989; Gutterman, 2002; Mistro et al., 2005). *A. desertorum* and *C. testiculata* may be

375   maintaining dormant seeds to spread the risk of germination over time, allowing seeds to wait for

376   more favorable germination conditions which may increase the chance of establishment and

377   survival. Another possibility for the over-representation of *A. desertorum* and *C. testiculata*

378   belowground is the simple fact that these plants were not frequently encountered aboveground

379   during data collection using the line-point intercept method due to their relatively small size (the

380   probability of a pin hitting a smaller plant is lower than the probability of hitting a larger plant)

381   and due to primarily actively growing much earlier in the season than when the aboveground

382   sampling occurred.

383   In contrast to the similarity and distance metrics, the NMDS suggested that the

384   germinable seed bank and aboveground vegetation were in fact moderately similar. One reason

385   for this disagreement is the organizational level of the aboveground vegetation used in

386   comparisons. For the similarity and distance metrics, relative abundances were compared at the

387   species-level. However, the NMDS compared the relative abundance of each species in the

388   germinable seed bank to the relative abundance of aboveground vegetation functional groups, i.e.

389   aboveground vegetation structure. Therefore, at the species-level the germinable seed bank and

390   aboveground vegetation communities were only moderately similar, but similarities were

391   considerably greater when comparing germinable seed bank species abundances to the

392   aboveground functional groups. There were a number of species that were only present above or

393   belowground (Tables A.1 and A.2) which decreased similarity between the germinable seed bank

394   and aboveground vegetation. However, the differences between each species present in either

395   community were no longer detected when using functional group as the aboveground

396   organizational level of comparison.

397   The germinable seed bank and aboveground vegetation tend to be more similar in annual

398   communities than in perennial communities (Thompson and Grime, 1979; Ungar and Woodell,

399   1993; Milberg, 1995; Bakker et al., 1996; Osem et al., 2006). NMDS results from the present

400   study did show a significant correlation between the annual germinable seed bank and

401   aboveground structure, but also a significant correlation between the perennial germinable seed

402   bank and aboveground structure. The unexpected correspondence between the perennial

403   germinable seed bank species and aboveground vegetation structure could simply be a function

404   of the comparison between species and functional groups. As displayed by the similarity and

405   distance metrics, the similarity between germinable seed bank and aboveground species

406   compositions was relatively low. However, comparing germinable seed bank species

407   composition to aboveground structure yielded the opposite result. Although the germinable seed

408   bank and aboveground vegetation were not similar at the species level, the germinable seed bank

409   species composition was similar to the aboveground vegetation functional group categories. For

410   example, both *Achnatherum hymenoides* and *Elymus elymoides* were positively correlated with

411   the aboveground perennial grass functional group.

412
413   *4.2. Aboveground community phase and microhabitat effects*
414
415
416   Shrub was the only functional group whose seed density was significantly affected by

417   microhabitat. The beneath shrub microhabitat contained more shrub seeds than interspaces,

418   which has been observed in other studies (Nelson and Chew, 1977; Guo et al., 1998; Marone et

419   al., 2004). Shrub seed densities tend to be higher under shrub canopies due to seeds falling

420   beneath and adjacent to the parent plant (phase I dispersal; Shaukat and Siddiqui, 2004). Shrubs

421   might have decreased wind velocity, physically trapping seeds beneath shrubs (Bullock and

422   Moy, 2004). Another explanation for higher beneath shrub densities is seeds could have been

423   transported by wind or water from interspaces and trapped in the litter beneath shrubs (phase II

424   dispersal; Chambers and MacMahon, 1994). However, if this was the primary reason we would

425   expect to have higher densities of other seed types beneath shrubs as well.

426   There are few studies investigating the spatial pattern of species richness of seeds in

427   desert shrub communities, but Li (2008) reported species richness was highest 2 m and 6 m from

428   shrubs. Results from the present research can neither corroborate nor contradict this finding.

429   Species richness was not significantly affected by any of the factors of interest.

430   The invasive grass *Bromus tectorum* was the most dominant annual grass on site.

431   However, annual grass seed density was not affected by aboveground community phase,

432   microhabitat, or the community phase x microhabitat interaction. Although we did not directly

433   examine the effects of *Bromus tectorum* on the seed bank, the invasion of *Bromus tectorum* can

434   create shifts to greater annual seed abundance (Young and Evans, 1975; Humphrey and Schupp,

435   2001) which can in turn affect the aboveground vegetation. Regardless of the differences in

436   perennial bunchgrass cover aboveground (community phase), annual grass seed density was not

437   affected—*Bromus tectorum* seed densities were relatively high as was aboveground cover

438   (Appendix A; Appendix B). Even if an invader can be eradicted aboveground, it may be

439   impossible to restore the vegetation community to the composition of an uninvaded community

440   (Vilà and Gimeno, 2007) due to invasive species persisting in the seed bank. Total seed density

441   and species richness, and seed density and species richness for all other functional groups

442   individually, were not significantly affected by aboveground community phase or microhabitat.

443   Seed banks of semiarid deserts can vary extensively spatially (Marone et al., 2004; Coffin and

444   Lauenroth, 1989) which may make it difficult to detect strong effects of these factors on seed

445   density and species richness.

446   In addition to seed density and species richness, the germinable seed bank species

447   composition was not strongly affected by community phase or microhabitat, or at least NMDS

448   did not detect such effects. Due to variability in seed dispersal patterns among species, distinct

449   germinable seed bank communities as a function of microhabitat and aboveground community

450   phase may not exist.

451   Prior to our research, the relationship between the seed bank and aboveground vegetation

452   had not yet been examined in cold desert plant communities. Our study found that seed

453   densities, species richness, and the germinable seed bank community composition were not

454 affected by aboveground community phase or, with the exception of shrub functional group seed

455 densities, microhabitat. Species compositions were moderately dissimilar when the germinable

456 seed bank and aboveground vegetation were compared at the species level but were moderately

457 similar when the germinable seed bank was compared to the aboveground vegetation functional

458 groups. These findings provide new insight into seed banks of cold deserts and their potential to

459 influence the aboveground vegetation.

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