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BURIAL INCREASES SEED LONGEVITY OF TWO *ARTEMISIA TRIDENTATA* (ASTERACEAE) SUBSPECIES [1]

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- *Premise of the study*: Seed longevity and persistence in soil seed banks may be especially important for population persistence in ecosystems where opportunities for seedling establishment and disturbance are unpredictable. The fire regime, an important driver of population dynamics in sagebrush steppe ecosystems, has been altered by exotic annual grass invasion. Soil seed banks may play an active role in postfire recovery of the foundation shrub *Artemisia tridentata*, yet conditions under which seeds persist are largely unknown.
- *Methods*: We investigated seed longevity of two *Artemisia tridentata* subspecies in situ by retrieving seed bags that were placed at varying depths over a 2 yr period. We also sampled naturally dispersed seeds in litter and soil immediately after seed dispersal and before flowering in subsequent seasons to estimate seed persistence.
- *Key results*: After 24 mo, seeds buried at least 3 cm below the soil surface retained 30–40% viability whereas viability of seeds on the surface and under litter declined to 0 and < 11%, respectively. The density of naturally dispersed seeds in the seed bank was highly heterogeneous both spatially and temporally, and attrition varied significantly by region.
- *Conclusions*: Our study suggests that *Artemisia tridentata* has the potential to form a short-term soil seed bank that persists longer than has been commonly assumed, and that burial is necessary for seed longevity. Use of seeding techniques that promote burial of some seeds to aid in formation of a soil seed bank may increase restoration potential.

Key words: *Artemisia tridentata*; nondeep physiological dormancy; restoration; seed burial; seed longevity; seed persistence; soil seed bank

Seed longevity and persistence in soil seed banks can compensate for effects of unfavorable environmental conditions on seedling germination over the long-term (Gutterman, 1994; Holmgren et al., 2006) and increase odds that viable seeds are available when conditions are optimal for recruitment. Seed banks may be especially important for population persistence in ecosystems where opportunities for seedling establishment and disturbance are unpredictable (Baskin and Baskin, 2001; Fenner and Thompson, 2005). Primary seed dormancy, the dormancy state of a freshly mature seed (Crocker, 1916; Baskin and Baskin, 2001), was widely assumed to be the only mechanism for a persistent seed bank but recent studies have shown that there is little correlation between seed dormancy and seed bank persistence (Thompson et al., 2003; Honda, 2008). If suitable conditions are not present to cue germination when primary

dormancy is broken, secondary dormancy may be induced (Bouwmeester and Karssen, 1992; Vleeshouwers et al., 1995; Baskin and Baskin, 2001), wherein seeds must experience proper cues for breaking dormancy again before they can respond to a germination cue. Viable seeds can persist in soil seed banks as a result of many interacting factors including dormancy state, germination cues or lack thereof, seed size, and burial (Thompson et al., 1993; Hulme, 1998; Hulme and Borelli, 1999; Ooi et al., 2007; Honda, 2008).

Artemisia tridentata Nutt. (big sagebrush) is an ecologically and economically important foundation shrub (Sands et al., 1999; Knick et al., 2003; Maher, 2007; Evans and Rollins, 2008; Miller et al., 2011) in one of the largest biomes in North America. Seeds of *A. tridentata* display characteristics of nondeep physiological dormancy (Baskin and Baskin, 2001) that can be broken by relatively short periods of cold stratification (Meyer and Monsen, 1991, 1992), and also can require light to varying degrees for germination (Meyer et al., 1990). It has been assumed that seeds will either germinate or perish within a growing a season and that seed banks are transient (persisting in the soil for less than one year). However, there is some evidence to suggest *A. tridentata* can form short-term persistent (persisting 1–5 yr) seed banks (Bakker et al., 1996; Thompson et al., 2003), but reports of its significance and magnitude disagree. On one hand, very little viable seed has been found in soil samples less than a year after natural seed dispersal (Hassan and West, 1986; Young and Evans, 1989) or broadcast-seeding (Chambers, 2000). On the other hand, repeated establishment of seedling cohorts for 2–4 yr following a one-time seed application (Schuman et al., 1998; Booth, 2002) and a large fire (Ziegenhagen and Miller, 2009) suggest the possibility of seed bank persistence for multiple years.

Historically, the sagebrush steppe ecosystem comprised over 63 million hectares of the Great Basin of North America (Miller and Eddleman, 2001; Knick et al., 2003). The ecosystem is threatened (Noss et al., 1995; West, 2000), due largely to several negative ecosystem effects (D'Antonio and Vitousek, 1992; Norton et al., 2004, 2007) associated with *Bromus tectorum* L. (cheatgrass) dominance of approximately 20 million hectares (Bradley and Mustard, 2005). Prior to *B. tectorum* invasion, fires were more complex (Bond and van Wilgen, 1996) and had return intervals on the order of decades to centuries (Whisenant, 1990; Miller and Rose, 1999; Miller and Tausch, 2001). *Bromus tectorum* invasion has reduced fire return intervals to less than a decade, lengthened fire seasons, and promoted more extensive burns (Whisenant, 1990; Johnson et al., 1999; Brooks and Pyke, 2001; Miller et al., 2011). The drastic change in the fire regime has brought about an alternative stable state (Westoby et al., 1989), making restoration of native vegetation and their community dynamics extremely difficult.

Expansion of invasive annual grasses has altered historic fire regimes to the point where a viable soil seed bank may play a larger role in population persistence of *A. tridentata*. In ecosystems where fire is a regular occurrence, plants species that are killed by fire depend on regeneration from seed after fires (Lavorel and Garnier, 2002; Pyke et al., 2010). Seeds may come from soil seed banks or from adult plants that persist after spatially complex fires (Ooi et al., 2006). Obligate-seeders are adapted to fire intervals that exceed their juvenile periods (Lamont et al., 1991), or else subsequent fires would eliminate postfire seedling cohorts before they were able to contribute to the population as reproducing adults. An increase in fire frequency or decrease in fire complexity may make obligate-seeders vulnerable to local extinction as seed banks deplete over time and no adult plants remain to repopulate areas (Bradstock et al., 1998; Pausas, 2001). Local regeneration of *A. tridentata* is limited by seed availability rather than seed production or germination (Daubenmire, 1975; Harniss and McDonough, 1976; Meyer and Monsen, 1992). As an obligate-seeder (Meyer, 2008), spatial and temporal patchiness of fires are important attributes for successful recolonization of burned areas by locally dispersed *A. tridentata* seeds. The prevalence of frequent large fires in *Bromus tectorum*-invaded habitat limits availability of seeds dispersed into the interior of burned areas, leaving seeds in soil seed banks as the primary natural source for re-establishment immediately following fires.

Mechanisms by which *A. tridentata* seeds may form a seed bank are not well understood. However, a light requirement for germination suggests burial could be such a mechanism. To our knowledge, there have been no direct field experiments or observations to test whether only buried *A. tridentata* seeds persist and/or remain viable in the field beyond one year. Our main objectives were to determine whether *A. tridentata* seeds have the potential to form a short-term persistent seed bank and, if so, how long seeds remain viable. We asked three questions to achieve our objectives:

1. How long can seeds remain viable?
2. Does seed longevity depend on a seed's depth in soil?
3. Does seed longevity change with environmental conditions?

MATERIALS AND METHODS

***Study areas**—Artemisia tridentata* is composed of three main subspecies: *Artemisia tridentata* Nutt. subsp. *tridentata* (basin big sagebrush), *A. tridentata*

subsp. *wyomingensis* Beetle and Young (Wyoming big sagebrush), and *A. tridentata* subsp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush). Our investigation of seed longevity was focused on two subspecies, *A. tridentata* subsp. *wyomingensis* (hereafter *A. t.* subsp. *wyomingensis*) and *A. tridentata* subsp. *vaseyana* (hereafter *A. t.* subsp. *vaseyana*). We experimentally buried seeds and sampled the soil for naturally dispersed seeds in field sites throughout the Great Basin for two years.

In August 2006, we selected six study sites in Oregon, Idaho, Utah, and Nevada (Table 1). Sites are representative of sagebrush communities and were chosen to capture variability across the Great Basin, with more mesic areas to the north and more arid to the south (West, 1983). At each site, we located one *A. t.* subsp. *wyomingensis* community, found in low- to midelevations in valleys and foothills on shallow soils, and one *A. t.* subsp. *vaseyana* community which typically occurs in higher elevations on cooler, wetter sites with deeper soils (Mahalovich and McArthur, 2004). Communities were chosen based on visual estimation of codominance by *A. tridentata* and native caespitose grasses, and low cover of *B. tectorum*. Prominent grasses included *Poa secunda* J. Presl (Sandberg bluegrass), *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), and *Elymus elymoides* (Raf.) Swezey (bottlebrush squirreltail).

We established a 35 m × 40 m plot in each community at least 20 m from the nearest road. These plots or communities ranged from 10–27 km apart within a site. Data on elevation, slope, aspect, and latitude/longitude were recorded; slope, aspect, and latitude were used in calculating potential direct incident radiation (PDIR) (McCune, 2007). Long-term average annual precipitation estimates for each plot were obtained with the PRISM Data Explorer (Parameter-elevation Regressions on Independent Slopes Model, PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA, http://www.prismclimate.org [accessed 31 Oct 2009]).

***Seed burial experiment**—*We evaluated seed longevity of each subspecies separately as this was not a reciprocal experiment. We placed seeds of a subspecies in their community and assessed their viability in a randomized complete block design with a two-way factorial treatment structure. Factors were seed depth with three levels (buried 3 cm below soil surface, at the soil surface beneath 2 cm of sagebrush leaf litter, and above soil and litter) and collection time with four levels (late spring after normal germination during the first season—April 2007; autumn around the time of seed dispersal and one year after placement—November 2007; after germination during the second field season—April 2008; and autumn at seed dispersal at the end of 2 yrs—November 2008). Each treatment combination was replicated 8 times for a total of 96 experimental units in each plot.

To keep the experiment manageable, we purchased source-identified seeds of both subspecies that had been collected by a certified commercial supplier (Granite Seed Co., Lehi, Utah, USA) in autumn 2005. Although this did not allow comparisons of genetic differences among populations, it allowed for comparisons among sites because all seeds of a subspecies came from a single population. Seeds were actually 1-seeded achenes (hereafter referred to as seeds), approximately 1-2 mm long and enclosed in a papery pericarp. Seed collections of this species often include plant material such as small twigs, leaves, and chaff in addition to seeds. Seeds lots were cleaned (separation of seed and nonseed material) using a series of sieves and blowers. The pericarp can be removed during the seed cleaning process (Booth et al., 1997) but this has minor effects on seed germinability (Bai et al., 1999). Because *A. tridentata* seeds were so small, we used seed bags to ensure that seeds could be retrieved. Seed bags were 5 × 5 cm and constructed from fine mesh (<0.5 mm opening), white polyester. We took measurements of light in- and outside bags on a bright, sunny day with a quantum sensor (Apogee Instruments, Logan, Utah, USA) and determined that the mesh allowed 85% ambient light penetration. We placed 100 seeds of a single subspecies in each bag using an automated seed-counter (± 0.52 seeds *A. t.* subsp. *wyomingensis* and ± 0.90 seeds *A. t.* subsp. *vaseyana*) after cleaning seed lots to about 95% seed by weight. A set of eight replicates was randomly selected during seed bag construction as a pretreatment control to determine initial viability of seeds placed in the experiment. Fresh seeds and seed bags were stored at 4°C at all times for the few months before they were deployed in the field.

In late November 2006, we located 96 *A. tridentata* shrubs (three depths x four collection times x eight replicates) with a minimum canopy size of 0.25 m² in each plot. Each bag was placed beneath a shrub 10 cm toward the main trunk or trunks from the outer canopy edge and directly beneath an inflorescence, and randomly assigned to one of twelve treatment combinations. After seed bags were retrieved from the field, they were stored at 4°C for up to one month until seeds could be examined and placed into categories: (1) recent

TABLE 1. Location and environmental characteristics of study sites.

Artemisia tridentata subsp. and site	Plot code	UTM			Precip[1] (cm)	Aspect (°)	Elevation (m)	Slope (%)	PDIR[2]	ARTR cover[3] (%)
		Zone	Easting	Northing						
wyomingensis										
E. Oregon	JUWY	11	415270	4843486	27.5	83	1072	11.9	0.77	17
W. Idaho	MHWY	11	592788	4801890	37.5	175	1096	4.6	0.84	25
E. Idaho	LLWY	12	273518	4789807	30.2	62	1451	2.3	0.79	13
N. Utah	SAWY	12	319756	4651825	30.5	269	1651	2.9	0.82	21
W. Utah	TOWY	12	374946	4451101	32.5	102	1903	3.4	0.84	32
E. Nevada	HUWY	11	735855	4329506	33.2	351	2034	5.7	0.78	34
vaseyana										
E. Oregon	JUVA	11	406674	4870576	32.2	150	1277	9.7	0.86	18
W. Idaho	MHVA	11	602396	4799358	50.5	108	1317	2.9	0.80	16
E. Idaho	LLVA	12	286703	4813701	40.6	77	1806	2.9	0.79	67
N. Utah	SAVA	12	307686	4647142	45.2	51	1919	4.6	0.79	33
W. Utah	TOVA	12	366248	4441482	42.9	352	1916	11.9	0.70	19
E. Nevada	HUVA	11	727196	4324108	40.2	231	2274	6.3	0.87	31

[1] Long-term annual precipitation averages (PRISM Normals 1971-2000 800m Normals, Parameter-elevation Regressions on Independent Slopes Model, PRISM Climate Group, http://www.prismclimate.org [accessed 31 Oct 2009])

[2] Potential direct incident radiation ($MJ \cdot cm^{-2} \cdot yr^{-1}$) (McCune, 2007)

[3] *Artemisia tridentata* cover

germination in situ – having evidence of either green cotyledons or a white radicle protruding from the seed (achene); (2) intact and viable; and (3) not intact. Because six months had elapsed between sampling dates, we were unable to determine the fate of missing seeds. Seeds that were unaccounted for were assumed to have decomposed, either because they had germinated or because they were nonviable. Seeds were checked for obvious fungal infection (i.e., hyphae visible under a dissecting microscope). Viability of intact seeds was tested by a tetrazolium (TZ) test using standard Association of Official Seed Analysts (2004) techniques and conducted by the Utah Department of Agriculture (State Seed Laboratory, Salt Lake City, Utah, USA). Because the purpose of this study was to assess seed persistence at varying soil depths over time, we use 'viability' to indicate the proportion of viable seeds that have not yet germinated as of the sampling date.

Soil sampling—We sampled the soil to determine whether naturally dispersed seeds persisted from one season to the next. We took 48 soil cores under big sagebrush shrubs (one core per shrub) within each of the 12 study plots. Samples were approximately 5 cm in diameter and 3 cm deep. We sampled twice during the growing season for two seasons (2006–07 and 2007–08), once immediately after seed dispersal (November) and again 9 mo later (August) before the next season's flower production. Soil cores were divided into litter and mineral soil fractions. Litter fractions were mixed with ca 300 g of sterile sand to increase water-holding ability of samples. Water was then added to both fractions, bringing them to field capacity, and cold-stratified in a dark cooler for 3–4 mo at 4°C. Because we quantified seed density by counting emerging seedlings, it was important to break primary dormancy in these seeds. Additionally, storing seeds in a cooler prevented them from decaying between collecting and growing out samples. After stratification, samples were spread in small trays and placed in an unheated greenhouse in Corvallis, Oregon during spring (February–April 2007 and 2008) and monitored for big sagebrush seedling emergence. Day temperatures ranged from 20.8–41.3°C and night temperatures ranged from −2.2–5.4°C. Samples received ambient light and were kept continuously moist until emergence of new seedlings stopped. We then mixed each sample to bring any potential ungerminated seeds to the surface and continued to water until emergence of new seedlings stopped once again. Germinated seeds were counted and discarded every few days.

Bag effect experiment—To account for potential effects of seed bags on seed viability or germinability, we reproduced field burial treatments with and without seed bags in an experiment conducted in a greenhouse. Topsoil and litter from an area adjacent to each field plot were collected in June 2008, and mixed together by subspecies. We sieved soil to remove large debris and rocks and homogenize across sites, then mixed it with sterile sand in a 1:1 ratio to use as potting media. All seeds (seed bags containing 100 seed each and sets of 100 free seeds) were subjected to a 21-day, cold stratification (4°C) in darkness before being placed in treatment pots. We were primarily interested in whether

seed bags prevented germination and subsequently bias results toward an overestimation of persistent seeds; therefore, we followed the minimum requirements to break dormancy in this species as defined by an International Seed Testing Association accredited laboratory (Sabry Elias, Oregon State University Seed Laboratory, Corvallis, Oregon, USA, personal communication). Seed bags and free seeds were placed in 5 × 5-cm pots, either 3 cm below the soil surface, on the soil surface under litter, or above 2 cm of litter. Control pots were filled with soil and topped with litter but contained no added seeds to control for seeds naturally present in field-collected soil. Treatments were replicated 6 times and pots placed in an unheated greenhouse in Corvallis, Oregon and monitored for germination. Day temperatures ranged from 24.0–44.1°C and night temperatures from 4.6–13.9°C. Newly germinated seeds were counted and discarded. After 1 mo, we extracted seeds from the soil medium of control and no bag treatment pots using a modification of the method by Malone (1967). Soil was first passed through sieves (2 mm, 1 mm, 425 μm openings) to obtain the seed-containing soil fraction. The fraction was mixed with a high-density 1 M sugar solution and centrifuged for 10 min at 2600 rpm. Seeds were manually sorted from the small amount of organic matter that floated to the top of the supernatant. Intact seeds from all treatments were sent to the Utah Department of Agriculture to test for viability.

Statistical analysis—Data were analyzed separately by subspecies using SAS 9.13 statistical software (SAS Institute, Cary, North Carolina, USA). Seed bag burial data were modeled using logistic regression with site, seed depth, and collection time as fixed effects and viability of intact seeds as the response variable. We analyzed only buried and litter treatments to better accommodate assumptions of a logistic regression (Andy Olstad, Oregon State University Statistical Consulting Laboratory, Corvallis, Oregon, USA, personal communication). We modeled seed bank data (number of germinable seeds) and bag effect data (number of viable seeds) with Poisson regression. Seed bank data were analyzed separately by year and fraction (litter or soil) because litter and soil fractions per sample were not spatially independent of one another. Site and collection time were used as fixed effects. Analysis of bag effect data were performed similarly with bag and seed depth as fixed effects. Bonferroni adjustments for posthoc multiple comparisons were applied where appropriate for all analyses.

RESULTS

Bag effect experiment—We found no naturally occurring seeds in field-collected soil of either subspecies for the control treatment; therefore, we concluded that any germinants or seeds found in soil for the no-bag treatment were from seeds that were added. On average, bagged seeds on the surface or under litter

had approximately four times higher viability compared to seeds that were free in soil under the same depth treatments (Fig. 1), primarily because free seeds had higher germination than bagged seeds. However, a similar proportion of bagged seeds and free seeds in the buried treatment remained intact and viable.

Seed burial experiment—Control seeds had an initial average viability of 91.6% (±1.4 SE) for *A. t.* subsp. *wyomingensis* and 81.1% (±2.6 SE) for *A. t.* subsp. *vaseyana*. No germination in situ occurred at the first spring collection and subsequent sampling revealed slightly more germination within burial treatments for both subspecies (Table 2). Viability of intact seeds dropped rapidly at all depths within the first 6 mo (Fig. 2 and 3), and surface seeds dropped to zero across almost all sites for both subspecies. The rate at which *A. t.* subsp. *wyomingensis* seeds lost viability depended on depth of seeds in the seed bank ($F_{1,301} = 22.59$, $P < 0.001$) and varied marginally among sites ($F_{5,301} = 2.04$, $P = 0.07$). For *A. t.* subsp. *vaseyana* the change in seed viability over time depended on both seed depth and site ($F_{5,282} = 2.69$, $P < 0.02$). Viability of intact seeds on the surface and under litter continued to decrease for the duration of the study but 29–36% and 30–40% (95% confidence interval) of

buried *A. t.* subsp. *wyomingensis* and *A. t.* subsp. *vaseyana* seeds, respectively, remained viable over the 24 mo period.

Soil sampling—The density of naturally dispersed seeds was highly variable among and within sites for the first year of sampling (Fig. 4). The change in seed density over time depended on site for *A. t.* subsp. *wyomingensis* (litter: $F_{5,564} = 2.16$, $P = 0.06$; soil: $F_{5,564} = 12.20$, $P < 0.001$) and varied across sites for *A. t.* subsp. *vaseyana* (litter: $F_{5,564} = 28.71$, $P < 0.001$; soil: $F_{5,564} = 63.26$, $P < 0.001$). There was more attrition of viable seeds in *A. t.* subsp. *wyomingensis* soil samples than litter samples, and more attrition overall compared to *A. t.* subsp. *vaseyana*. Sampling in the second season revealed considerably lower seed density than was observed in the first season. In November 2007 we found no viable seeds for *A. t.* subsp. *wyomingensis* in litter or soil samples and only three out of 576 samples, from three different sites (western Idaho—MHWY, eastern Idaho—LLWY, and eastern Nevada—HUWY), yielded any viable seeds in August 2008. Litter samples from only one *A. t.* subsp. *vaseyana* site (eastern Oregon—JUVA) had viable seeds in November 2007; however, in August 2008 just before seed dispersal, we found an average of 11-53 viable seeds/m² for *A. t.* subsp. *vaseyana* in litter and soil samples from three regions (eastern Idaho—LLVA, northern Utah—SAVA, and eastern Nevada—HUVA).

DISCUSSION

Ours is the first study to experimentally document that *A. tridentata* has the potential to form a seed bank and that seed longevity is greatly enhanced by burial of seeds in the soil. This is in contrast to previous assertions that *A. tridentata* seeds do not stay viable for more than a season. The proportion of viable buried seeds was fairly constant for both subspecies throughout the 2 yr study period. Seeds on the surface and under litter steadily decreased in viability over time but varied by site as to how quickly this happened. We also observed low densities of viable seeds in litter and soil fractions of both subspecies 9 mo after natural seed dispersal, persisting longer than previous studies had indicated.

Seed bank persistence is affected by many things, both biotic and abiotic environmental factors and traits inherent to the seed itself. Seeds collected from cold winter sites are nearly 100% light-requiring for germination, perhaps as an adaptation to prevent seeds from germinating under snow (Meyer et al., 1990). Seeds of both subspecies used in our experiment were collected from areas with cold winters; therefore most of these seeds likely needed a light cue for germination. Buried seeds of the two subspecies in our study experienced two winter seasons where soil temperatures 3 cm below the surface can range from 0 to 10°C even in autumn (Evans and Young, 1972). This may have been cold enough to break primary dormancy (Meyer et al., 1990; Meyer and Monsen, 1991) but, because we did not test for germinability of intact seeds, we cannot say for certain whether they were dormant or merely lacking a germination cue.

Burial of seeds can ameliorate environmental effects and increase longevity of seeds that might otherwise be lost to death or germination (Hulme and Borelli, 1999; Facelli et al., 2005). For example, diurnal temperature fluctuations become increasingly dampened by soil depth (Pierson and Wight, 1991). This can increase seed longevity since temperature is
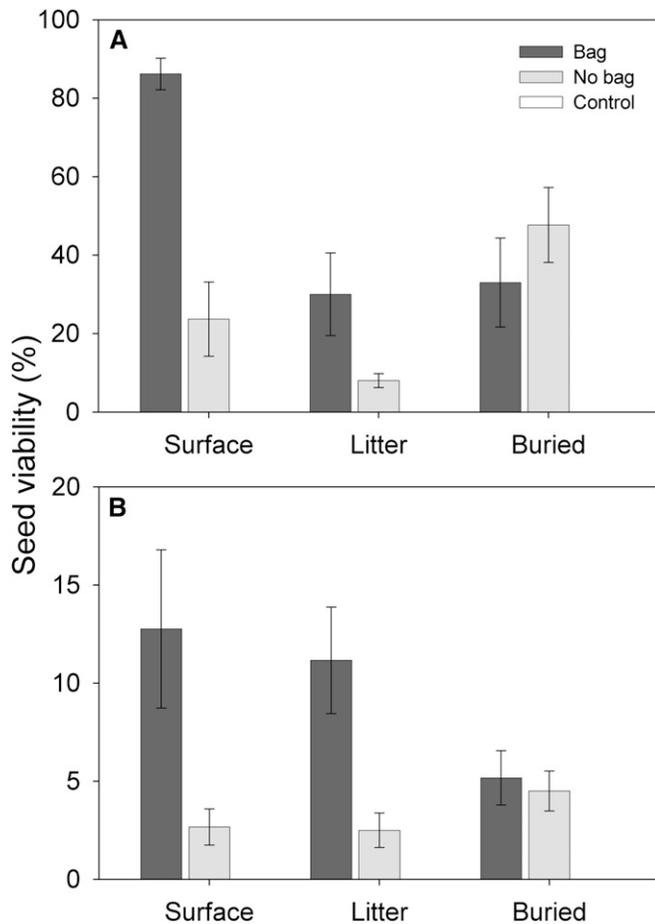

Fig. 1.   Effect of mesh bags on mean seed viability of (A) *Artemisia tridentata* subsp. *wyomingensis* and (B) *A. t.* subsp. *vaseyana* after one month in a greenhouse. Note different scales on Y-axes. Bars represent ±1 SE.

TABLE 2. Mean percent seed germination (% ±1 SE) by subspecies and seed depth for seed burial experiment. Seeds were deployed in mesh bags at field sites in November 2006. Values are determined from seeds that had germinated at the time of collection and do not include seeds that may have germinated well before the sampling date and had since decayed and/or disappeared.

Artemisia tridentata subsp. and seed depth	Collection (% ±1 SE)			
	Spring 2007	Autumn 2007	Spring 2008	Autumn 2008
wyomingensis				
Burial	0 (0)	2.24 (0.75)	0.95 (0.47)	0.89 (0.37)
Litter	0 (0)	2.08 (0.75)	0.08 (0.06)	0 (0)
Surface	0 (0)	0.11 (0.05)	0 (0)	0 (0)
vaseyana				
Burial	0 (0)	0.63 (0.18)	0.19 (0.08)	0.26 (0.14)
Litter	0 (0)	0.09 (0.06)	0.09 (0.07)	0 (0)
Surface	0 (0)	0.03 (0.03)	0 (0)	0 (0)

one of the factors that impacts the rate at which seeds age (Walters, 1998). Crist and Friese (1993) determined that decomposition and attack by fungi were responsible for the greatest decrease in seed viability among shrub-steppe species during winter, with the greatest decrease occurring in *A. tridentata*. We determined that more than 75% of all surface and litter samples showed signs of fungal infection whereas less than 50% of buried seeds were infected. We found a higher proportion
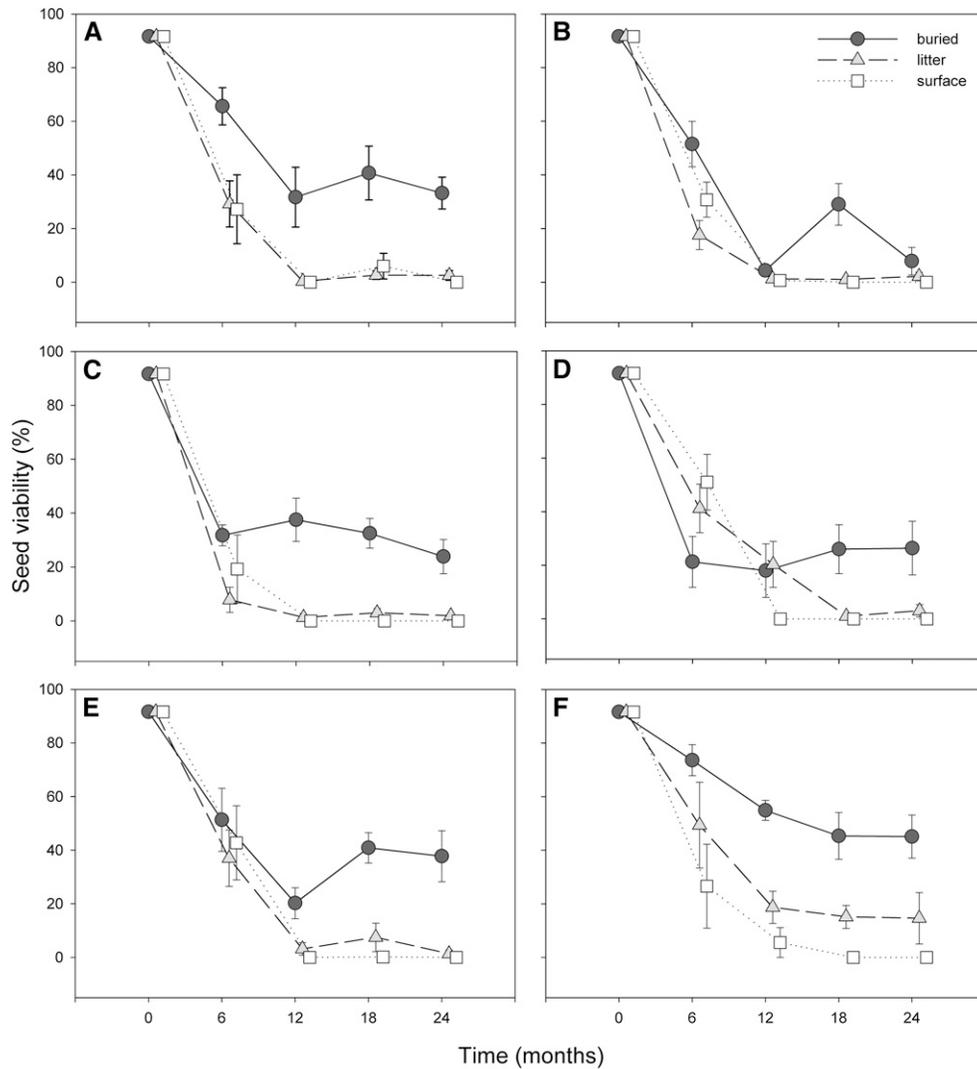

Fig. 2. Effect of seed depth on mean seed viability of *Artemisia tridentata* subsp. *wyomingensis* over a period of 24 mo in (A) eastern Oregon, (B) western Idaho, (C) eastern Idaho, (D) northern Utah, (E) western Utah, and (F) eastern Nevada. Bars represent ±1 SE.
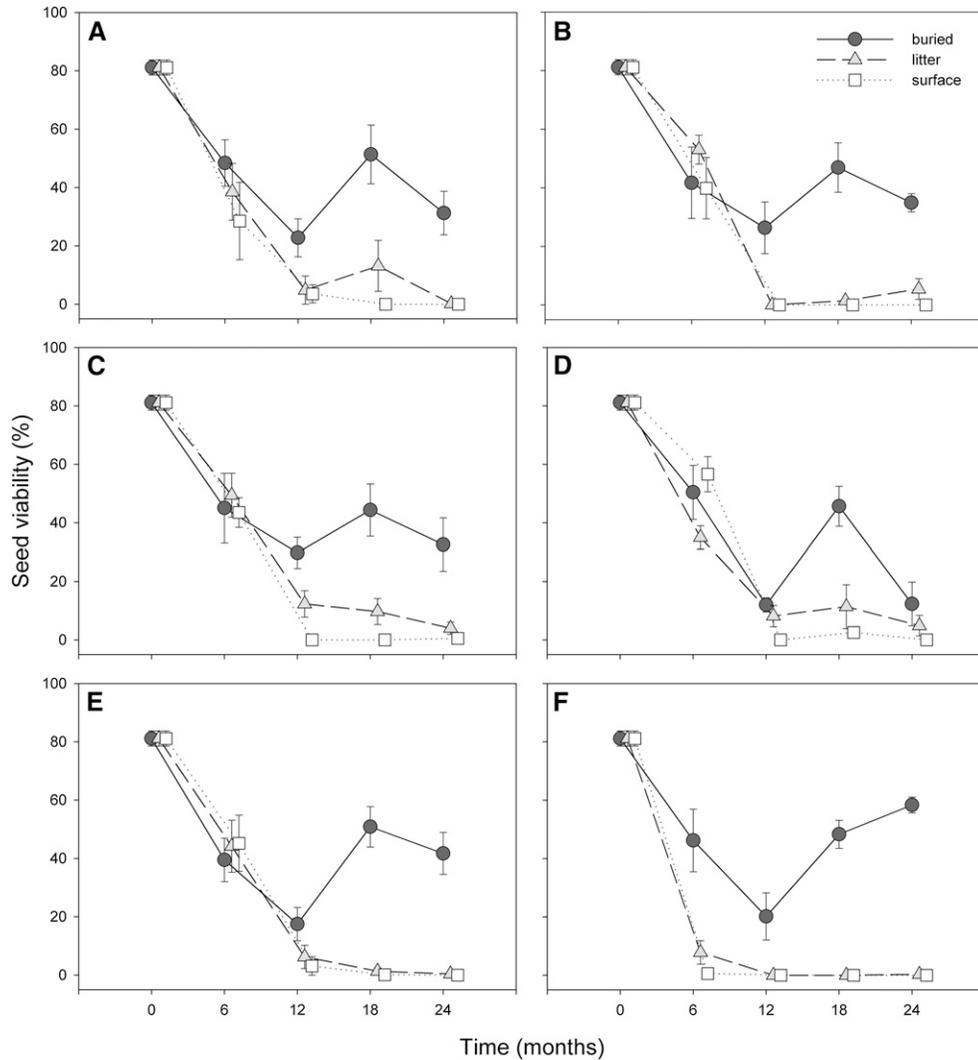
Fig. 3.   Effect of seed depth on mean seed viability of *Artemisia tridentata* subsp. *vaseyana* over a period of 24 mo in (A) eastern Oregon, (B) western Idaho, (C) eastern Idaho, (D) northern Utah, (E) western Utah, and (F) eastern Nevada. Bars represent ±1 SE.

of moldy seeds in *A. t.* subsp. *vaseyana* samples than *A. t.* subsp. *wyomingensis* samples after winter, and seed bank sampling consistently yielded more viable seeds of *A. t.* subsp. *vaseyana* in the soil fraction than in the litter fraction. This may explain why germination was slightly higher in buried treatments than in litter or surface treatments. Fungal attack may have left comparatively few viable seeds available for germination in litter and surface treatments after spring 2007. We could only document germination that occurred at the time of each collection so these results do not provide an accurate picture of seed loss due to germination vs. other factors.

Seed bags used in our study affected the microenvironment of seeds. These bags reduced ambient light by about 15% and may have inhibited seed germination, and thus increased the proportion of viable seeds in surface and litter treatments. This is an important technical finding because numerous seed bank studies have used mesh bags in surface or near-surface burial treatments to assess seed bank longevity. However, in the current study, buried seeds were unaffected by this design artifact

and may represent the potential maximum viability of seeds buried beneath the soil surface. There is also the possibility that these mesh bags maintained a higher level of moisture and potentially increased the risk of fungal infection through unnaturally high seed densities (Van Mourik et al., 2005) which would result in a conservative estimate of seed persistence. Alternatively, seed bags could inhibit macroinvertebrates in the soil and litter from preying on or damaging seeds, resulting in overestimation of seed persistence. Though we did not add soil to seed bags when they were deployed, we did observe that buried bags contained soil that was of uniform particle size upon retrieval. This may have provided a similar microenvironment and thus veiled potential heterogeneity in seed persistence within and across regions. Much like safe sites for seed germination, the microenvironment likely plays a role in the patchiness of a persistent soil seed bank.

Estimates of naturally occurring germinable seeds for the 2006–07 growing season varied among and within both subspecies, and there was high interannual variation in our two years of sampling. Many factors may impact *A. tridentata* seed
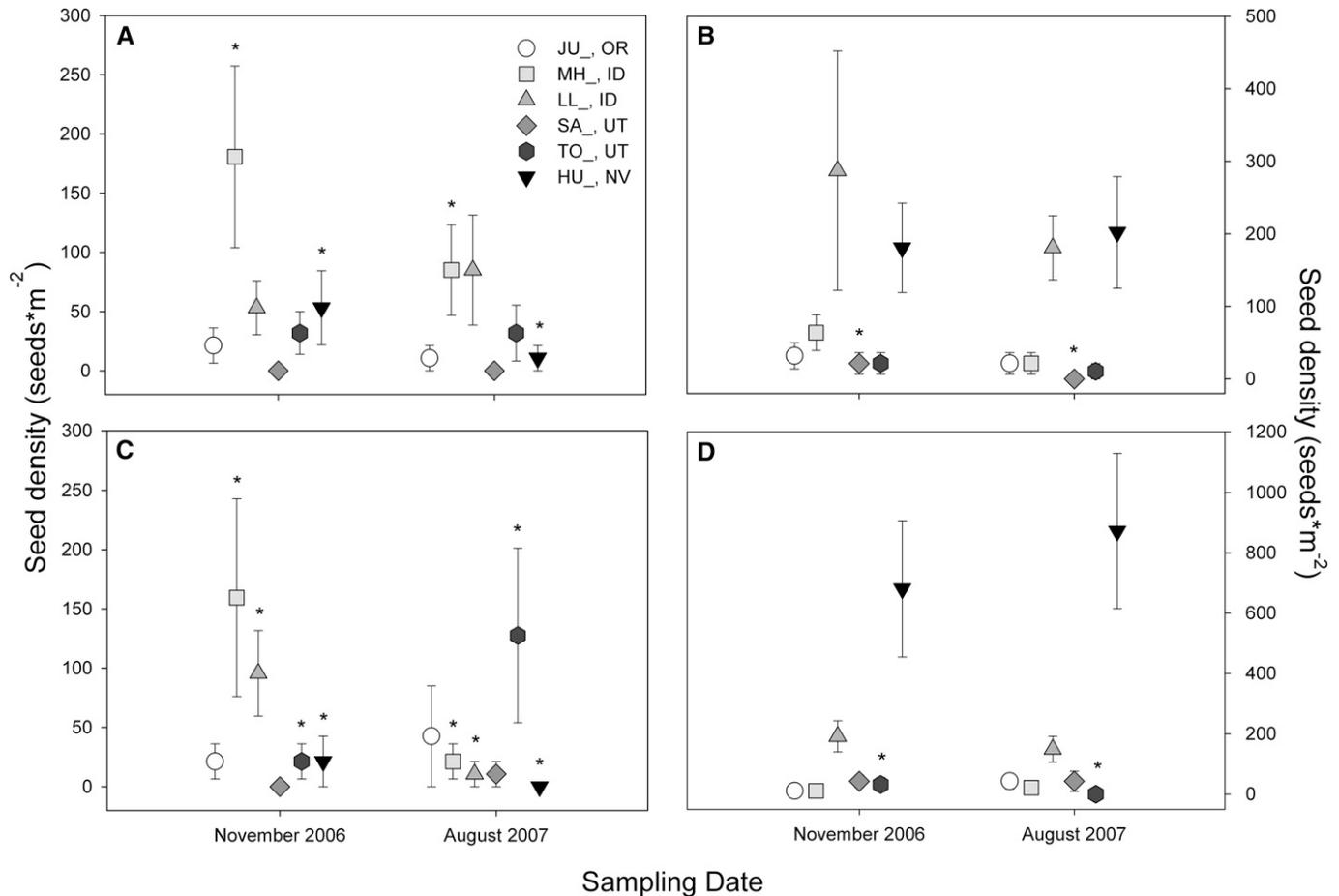
Fig. 4.   Mean seed density for (A,C) *Artemisia tridentata* subsp. *wyomingensis* and (B,D) *A. t.* subsp. *vaseyana* sites in (A,B) litter and (C,D) soil fractions. Within a site, asterisks indicate a significant difference in seed density between sampling periods. Graphs include data from the first year of sampling only. Note different scales on Y-axes. Bars represent ±1 SE.

production including browsing (Wagstaff and Welch, 1991), disease (Welch and Nelson, 1995), and dry years (Young et al., 1989). Abortion of seeds and fruits is a strategy that plants may adopt to compensate for resource limitation (Pyke, 1989). This may explain why there were lower densities of seeds in the soil during the second year as compared to the first year. Precipitation during the 2006-07 growing season was roughly 73% and 76% (*A. t.* subsp. *wyomingensis* and *A. t.* subsp. *vaseyana*, respectively of the long term average for those sites (1971-2000 Normals, climate data from PRISM Climate Group), and would have affected seed production in the second year of the study. We found much higher seed densities in autumn 2006, which had been influenced by annual precipitation that was slightly higher than long-term averages. Differences in biotic and abiotic characteristics between sites likely account for differences in soil seed density. For example, both litter and soil fractions of *A. t.* subsp. *wyomingensis* in western Idaho (MHWY) lost a significant number of viable seeds between sampling periods during the first season. Among *A. t.* subsp. *wyomingensis* communities, this site has the highest average annual precipitation and could have resulted in a higher incidence of fungal infection. However, because seed longevity is affected by many interacting factors it is difficult to identify specific characteristics of our study sites that may have influenced loss of viable seeds from the soil.

We determined density of naturally occurring seeds by germinating *A. tridentata* seeds from soil and litter cores instead of extracting seeds physically because the latter method was very labor intensive given our large number of samples. However, the germination method may underestimate seed persistence because dormant seeds or seeds that do not receive a germination cue will remain undetected in samples (Thompson et al., 2003). Furthermore, less than 25% of samples at all sites yielded germinable seeds despite taking samples directly beneath the inflorescence of an *A. tridentata* shrub. Young and Evans (1989) determined that the dispersal pattern of *A. tridentata* seeds in their study area was skewed to the east due to prevailing winds from the west. We did not take dispersal direction into account when taking soil samples. Buried seeds can be extremely patchy and the number of samples needed for density estimation increases as patchiness increases (Fenner and Thompson, 2005). Our *A. t.* subsp. *wyomingensis* estimates were an order of magnitude higher than estimates by Hassan and West (1986) though they took pains to extract all seeds from their samples prior to testing for viability. Our estimates were an order of magnitude lower than estimates by Young and Evans (1989) who determined seed persistence in the same manner we did. No viable seeds were found in the soil by 6 mo after dispersal by either study. Future studies of seed persistence in this species may warrant sampling using a more stratified random approach in addition to increasing the number of samples taken.

Density estimates of viable seeds presented here and in previous studies using similar sampling techniques may not give an accurate picture of seed persistence in this species because of the high clumping observed within and across regions in our study.

Naturally occurring soil disturbances could enhance seed bank persistence by incorporating a portion of seeds into the soil and potentially bringing seeds to the surface in subsequent years. Disturbances such as frost-heaving or burrowing by subterranean mammals could displace seeds from the surface to beneath the soil surface. Livestock grazing during or immediately after seed dispersal in the late-autumn or early winter may also enhance seed burial through hoof action turning or depressing soils (Winkel et al., 1991) and has been shown to increase *A. t.* subsp. *wyomingensis* seedling emergence under certain conditions (Eckert et al., 1986; Winkel and Roundy, 1991), potentially by turning up previously buried seeds. Young et al. (1990) found that texture of soil surfaces can change from autumn to spring through a winnowing action of wind. They suggest that *A. tridentata* seeds are affected by wind in the same manner as sand-sized particles of granitic soils and may become buried. The same processes that promote burial of *A. tridentata* seeds may operate to bring seeds to the surface.

Restoration efforts of sagebrush steppe often involve aerial seeding, which would leave many seeds on the surface. Aerial seeding of *A. tridentata* can result in poor shrub establishment (Dalzell, 2004). However, after seeds were broadcast onto the surface of a mulch layer, seedling emergence of *A. tridentata* through four postseeding growing seasons (Booth, 2002) indicates that some portion of the seeds may have worked into the soil over time. Providing a soil surface disturbance or mulch that aids in seed burial may increase restoration success. Restoration methods that ensure seed contact with soil such as pressing seeds into the soil surface (Pyke, 1996), creating microdepressions in the soil (Haferkamp et al., 1987), and harrowing or raking (Turner et al., 2006) can greatly increase seedling establishment. An unintended consequence of some of these methods may be burial of a small percentage of seed, which had long been thought to be undesirable. Our results suggest that there may be a middle ground between surface exposure and deep burial that maximizes restoration potential. We argue that techniques to help *A. tridentata* seeds remain viable in the soil as a hedge against unfavorable germination or establishment conditions may be one of the keys to long-term restoration success, and additionally may also spare seeds from incineration during wildfires (Laterra et al., 2006). Mixing high densities of *A. tridentata* seeds into seed drills for intentional burial, combined with broadcasting seeds onto the surface, may provide a seed source for years and, in the long-term, be more economically feasible than reseeding annually. However, if the mechanism for a persistent buried seed bank is lack of a light cue, then this tactic may work only with cold-adapted populations that are particularly dependent on light cues for germination.

In conclusion, our results indicate that dynamics of seed viability over time are similar in these two subspecies of *A. tridentata* and depend on depth of seeds in the soil. After the initial loss of seeds, most probably due to germination of physiologically nondormant fraction, both subspecies exhibited patterns of a steadily decreasing abundance of viable seeds on the surface and beneath litter. However, 30–40% of buried seeds remained viable across all sites for at least 24 mo. Our study suggests that reseeding techniques that promote burial of some seeds in the soil may increase restoration success.

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