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Germination phenology of some Great Basin native annual forb species

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Abstract

Great Basin native plant communities are being replaced by the annual invasive cheatgrass *Bromus tectorum*. Cheatgrass exhibits a germination syndrome that is characteristic of facultative winter annuals. Although perennials dominate these communities, native annuals are present at many sites. Germination timing is often an important predictor of competitive interactions, and might determine whether the use of annual species in restoration efforts will be successful. I used a laboratory experiment to determine whether a suite of native annuals exhibit winter or spring annual germination syndromes. Seeds of *Amsinckia menziesii* var. *intermedia*, *Amsinckia tesselata*, *Blepharipappus scaber*, *Descurainia pinnata*, *Eriastrum sparsiflorum*, *Lappula occidentalis*, *Mentzelia veatchiana* and *Plagiobothrys tenellus* were tested for dormancy, and for responsiveness to light, cold stratification and dry after-ripening. Species that would be expected to be most similar to cheatgrass are those that have no requirement for cold stratification and are therefore likely to germinate under autumn or winter conditions. The species that clearly met this criterion in this laboratory study were *A. menziesii* var. *intermedia*, *A. tesselata*, *D. pinnata* and *L. occidentalis*. In contrast, *B. scaber*, *E. sparsiflorum*, *M. veatchiana* and *P. tenellus* had their highest germination after cold stratification and would be expected to be spring germinators. *Blepharipappus scaber* was not coaxed out of dormancy to a great degree by any of the treatments I applied and may exhibit cue-non-responsive dormancy. Field seed burial experiments, as well as experiments examining the competitive ability of these annuals versus cheatgrass will further inform us about their potential for success in restoration seedings.

Keywords: annual, *Bromus tectorum*, forb, germination, Great Basin, restoration.

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Introduction

Cheatgrass *Bromus tectorum* is rapidly replacing Great Basin native plant communities (Pellant *et al*. 2004); an invasion that is enormous in its extent (D'Antonio & Vitousek 1992) and that has disastrous consequences for ecosystem function (Whisenant 1990). Historically, these communities were primarily dominated by perennials, particularly sagebrush (*Artemisia* spp.) and perennial bunchgrasses. However, many contain native annuals that, at good condition sites, can form a significant component of post-fire community recovery (Humphrey & Schupp 2001), particularly at previously uninvaded, recently burned sagebrush sites. At these sites, native annuals appear to be filling the niche often occupied by cheatgrass after disturbance. When subjected to competitors that are exploiting the same niche, an invasive species may be at a competitive disadvantage (Fargione *et al*. 2003; Zavaleta & Hulvey 2007). In a restoration context, native annuals may also be better suited to conditions in post-fire disturbed sites than late seral species. Life-history theory suggests that a short lifespan and early reproduction should be correlated with the degree of habitat disturbance (Grime 1977) and this has frequently been supported by empirical studies (Canals *et al.* 2005; Goergen & Chambers 2009). Attributes of Great Basin post-fire disturbances that might favor annual species include available nitrogen and light (Rau *et al*. 2008). Despite the ecological appropriateness of using annuals in restoration, species

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seeded in sagebrush shrublands are generally long-lived perennials and shrubs, and native annuals have not yet been used. For this reason, their basic biology and germination requirements are less well understood than those of perennials.

Germination phenology is an essential component of an annual species' niche, with profound influences on competitive outcomes (Fowler 1984; Rice & Dyer 2001). Germination phenology also influences reproductive output (Narita 1998), which is the most important component of an annual species' life history. Cheatgrass exhibits a germination syndrome that is characteristic of facultative winter annuals. It has some degree of dormancy at dispersal, and that dormancy is broken by dry after-ripening (Allen *et al*. 1995; Beckstead *et al*. 1996). If seeds do not encounter appropriate conditions for germination in the autumn, they appear to re-enter dormancy, but become non-dormant again in the spring (S. Meyer, pers. comm., 2009).

In general, dormancy tends to be a more important feature of the life history of annual species than perennial spedies because their above-ground life-history stages are more ephemeral (Kalisz & McPeek 1992; Doak *et al*. 2002). Dormancy in annual species is broken in response to environmental cues that allow for germination at the time when seedlings are most likely to survive (Harper 1977). There are some general patterns in germination phenology of annuals. For example, obligate winter annuals germinate in autumn and tend to exhibit cyclic dormancy that allows them to re-enter dormancy over winter (Baskin & Baskin 1973; Baskin *et al*. 1992; Haferkamp *et al*. 1994). Facultative winter annuals can germinate in either autumn or spring (Roberts & Neilson 1982; Baskin & Baskin 1989; Boutin & Harper 1991) and spring annuals generally germinate in spring or summer (Baskin & Baskin 2001). Winter annuals would be expected to have dormancy at dispersal that is broken by a period of hot, dry treatment simulating summer conditions (dry after-ripening; Masuda & Washitani 1992; Walck *et al*. 2008), whereas spring annuals would be expected to be responsive to a period of cold, wet treatment simulating winter conditions (cold stratification; Baskin & Baskin 1988). Facultative winter annuals might exhibit polymorphism within a population in dormancy levels in response to particular conditions (Baskin & Baskin 1983).

Great Basin native annual species with the ability to germinate in the autumn would be more likely to occupy a niche similar to that of cheatgrass. Species that germinate in the autumn with *B. tectorum* are able to accumulate biomass and establish roots that might provide a competitive advantage relative to spring germinators. Thus, for the present study, I selected native annual species that I observed to be part of the post-disturbance flora in Wyoming sagebrush (*Artemisia tridentata* var. *wyomingensis*) plant communities in western Nevada and that produced seed in 2007 and/or 2008. These species were *Amsinckia menziesii* var. *intermedia* (Boraginaceae), *Amsinckia tesselata* (Boraginaceae), *Blepharipappus scaber* (Asteraceae), *Descurainia pinnata* (Brassicaceae), *Eriastrum sparsiflorum* (Polemoniaceae), *Lappula occidentalis* (Boraginaceae), *Mentzelia veatchiana* (Loasaceae) and *Plagiobothrys tenellus* (Boraginaceae)

To the best of my knowledge none of these species has been formally assessed for germination requirements to date. In fact, the germination requirements of native annuals in cold deserts have been little studied in general. In contrast, multiple species of *Sonoran* (Adonakis & Venable 2004) and other hot desert annuals (Freas & Kemp 1983; DeFalco *et al*. 2003) have been studied over the course of many years. Until now, native annuals of cold deserts have not been the focus of seed research.

Many factors, including temperature, light, water availability and the identity and quantity of gases and chemicals in the soil regulate the breaking of dormancy in seeds, but in temperate regions, temperature is usually the overriding factor regulating dormancy break when soil moisture is sufficient (Baskin & Baskin 2001). Therefore, in addition to using light treatments, I focused on the effects of temperature on germination in these species of interest.

With the goal of identifying species that may have a germination phenology similar to that of cheatgrass, I screened these eight species to determine whether they exhibit dormancy and, if so, whether it is broken by dry after-ripening, as would be expected for obligate and facultative winter annuals, or if it is broken by cold stratification, as would be expected for spring annuals.

Materials and methods

Germination phenology laboratory experiments

Ripe seeds were collected as shown in Table 1 and stored at room temperature until the experiments commenced. All seed lots from an individual site were mixtures of seeds from at least 20, usually more, maternal plants. All seed lots were assessed for viability using a tetrazolium test (Association of Official Seed Analysts 1988). For each species, four samples of 50 seeds were soaked in deionized water overnight. The seeds were then pierced and soaked overnight in a solution of 1% 2,3,5-triphenyl tetrazolium chloride. Finally, embryos were assessed for staining. Guidance on embryo morphology for each species was taken from Martin (1946).

Seeds were checked for dormancy and light responsiveness using a 4-week germination test in Petri dishes. For each species, four replicate dishes of 25 seeds each were placed in fluorescent light and four were placed in the dark (wrapped in aluminum foil) in a Percival growth

Table 1 Species, locality, month of collection, storage prior to the start of the experiments, and viability for each seed lot used in the experiments

Species	Locality	Month	Storage time (months)	Viability (%)
Amsinckia menziesii var. *intermedia*	Keystone Canyon, Washoe County, NV	June 2008	9	89.9 ± 5.4
Amsinckia tesselata	Keystone Canyon, Washoe County, NV	June 2008	9	94.0 ± 4.7
Blepharipappus scaber	Keystone Canyon, Washoe County, NV	June 2008	9	77.0 ± 8.7
Descurainia pinnata	White River Valley, White Pine County, NV	June 2007	12	90.2 ± 2.4
Eriastrum sparsiflorum	White River Valley, White Pine County, NV	June 2007	9	99.0 ± 2.0
Lappula occidentalis	White River Valley, White Pine County, NV	June 2007	12	92.9 ± 2.6
Mentzelia veatchiana	Keystone Canyon, Washoe County, NV	June 2008	9	50.5 ± 11.7
Plagiobothrys tenellus	Balls Canyon, Sierra County, CA	June 2007	9	95.2 ± 3.5

chamber under a constant 20°C with an 8-h photoperiod. The seeds were placed on a moistened blue germination blotter (Anchor Paper, St Paul, MN, USA). Tap water was added to the blotters as needed to maintain moisture during the experiment. Germinated seeds were counted and removed from the dishes weekly. Seeds were considered to have germinated if the radicle was visible. Seeds in the dark treatment were checked under a green 'safe' light (Baskin & Baskin 2001).

Seeds were also tested for responsiveness to dry after-ripening and cold stratification. The dry after-ripening treatment consisted of subjecting four replicates of 25 seeds per species to storage in sealed glass jars in a 40°C incubator for 4 weeks. At the end of each week, six seeds per dish were checked for dormancy by placing them on wet filter paper in a 20°C incubator for 1 week. For the cold stratification treatment, four replicates of 25 seeds each were placed in Petri dishes with wet filter paper at 2°C and checked for germination weekly by moving six seeds to a new dish in the 20°C incubator for 1 week. Four weeks was used as the stratification period because seeds from these low elevation sites in the western Great Basin do not experience long periods under snow or months below freezing temperatures. Viability testing was done on these seed lots during March 2009. Germination experiments were conducted from 20 July 2008 to 30 August 2008.

There was an exception to the above for *M. veatchiana*, the two *Amsinckia* species and *B. scaber*, which were collected (Table 1) and tested for viability (December 2008) and germination (12 March 2009 through to 3 April 2009) at a later date than the other species. For these species, each dish contained 50 seeds, and 10 seeds were taken out of the after-ripening and cold stratification treatments per dish each week. More seeds were used in this experiment because more were available from these seed lots than from the lots used in the earlier experiment.

At the end of the experiment, the germination percentage was calculated using the number of viable seeds as follows:

$$\text{germination percentage} = (\text{number of germinated seeds} / \text{number of viable seeds}) \times 100 \quad (1)$$

The percentage of viable seeds germinating per dish was rank transformed and used as the response variable in a general linear model (GLM) analysis (PROC GLM, SAS 9.0; SAS Institute, Cary, NC, USA). Species were analyzed separately and treatment was the predictor in each analysis. The treatments were compared by species using planned, independent contrasts. Because the light and dark constant temperature treatments were intended to be a dormancy check as well as a test for light responsiveness, the germination percentage under the light treatment is assumed to indicate the level of dormancy at the time of germination testing (i.e. either after some months of dry storage or under fresh conditions). The exception to this is when germination is significantly higher under the dark treatment, in which case germination in the dark is used as the baseline. Therefore, the results of the stratification and after-ripening treatments are compared with these baseline levels of dormancy.

Germination rate data were calculated as the percentage of germinants per dish per week, adjusted using viability numbers. Rather than looking at an index of rate (e.g. calculated as time to 50% germination per dish, which does not take dishes with no germinants into account) I examined these data using germination curves.

Fresh seed dormancy assay

The ultimate goal of the present study was to determine whether there are native annual species that can both compete with cheatgrass and behave as suitable candidates for use in large-scale restoration projects. Seed lots were subjected to experimental treatments approximately 1 year after collection and dry storing these species at room temperature prior to testing simulates the conditions they will experience in a restoration setting.

Table 2 Species, locality, month of collection, viability, and number of seeds used per dish for each seed lot used in the fresh seeds assay

Species	Locality	Month	Viability (%)	Seeds per dish
Amsinckia menziesii var. *intermedia*	Keystone Canyon, Washoe County, NV	June 2009	88.4 ± 4.0	50
Amsinckia tesselata	Keystone Canyon, Washoe County, NV	July 2009	83.4 ± 9.1	50
Blepharipappus scaber	Keystone Canyon, Washoe County, NV	July 2009	67 ± 20.6	25
Descurainia pinnata	Steptoe Valley, White Pine County, NV	July 2009	90.2 ± 3.3	50
Eriastrum sparsiflorum	Evans Canyon, Washoe County, NV	June 2009	87.3 ± 10.2	50
Lappula occidentalis	Steptoe Valley, White Pine County, NV	July 2009	96.1 ± 2.7	50
Mentzelia veatchiana	Keystone Canyon, Washoe County, NV	June 2009	90.3 ± 6.5	50
Plagiobothrys tenellus	Balls Canyon, Sierra County, CA	June 2009	55.2 ± 8.4	25

However, to truly understand the biology of these seeds, one must examine the dormancy status at dispersal (Baskin & Baskin 2001). Room temperature after-ripening is sufficient to break dormancy for some species, such as *Bromus tectorum* (Allen *et al*. 1995), but many species require higher temperatures (such as they would experience in the field) for after-ripening (Baskin & Baskin 2001). These higher temperatures were simulated by our 40°C after-ripening treatment.

To examine the germination requirements of fresh seeds, an unreplicated dormancy assay was conducted to determine whether fresh seeds of each species have dry after-ripening requirements that have been satisfied by the storage prior to the first experiment. In 2009, seeds of each species were collected, cleaned and assessed for dormancy within 1–2 months of collection in a growth chamber at 15°C for 2 weeks, a standard time period for assessing dormancy status. The seed lots used for this experiment are shown in Table 2. Either 50 or 25 seeds per species were placed in a dish (depending on seed availability; see Table 2) as described for the experiments above, and one dish per week was evaluated for germination. This qualitative test is referred to as the fresh seeds dormancy assay throughout the rest of this paper.

Results

Laboratory germination phenology study

Amsinckia menziesii var. *intermedia* This species showed moderate levels of dormancy after 9 months of dry storage. The percentage of viable seeds germinating in the light treatment was 40.0 ± 11.2% (Fig. 1). There was a strong light response (light *vs* dark MS = 5751.28, $F_{1,3} = 85.77$, $P < 0.0001$); only 1.7 ± 3.3% germinated in the dark. *Amsinckia menziesii* var. *intermedia* did not respond to stratification (light *vs* stratification MS = 11.28, $F_{1,3} = 0.17$, $P = 0.6889$) and after-ripening appeared to induce dormancy; germination percentage dropped to 13.9 ± 7.5% in this treatment (light *vs* after-ripening MS = 1596.13, $F_{1,3} = 23.80$, $P < 0.0004$; Fig. 1). Results of the GLM are shown in Table 3.

Only in the light treatment did germination continue to increase dramatically after the first week. The germination percentage in this treatment went from 8.3 ± 8.0% after 1 week to 40.0 ± 11.2% after 4 weeks (Fig. 2).

Amsinckia tesselata This species was also somewhat dormant after 9 months of dry storage. The percentage of seeds germinating in the light treatment was 40.9 ± 15.3% (Fig. 1). As with *A. menziesii* var. *intermedia*, there was a strong light response (light *vs* dark MS = 4418.00, $F_{1,3} = 32.14$, $P < 0.0001$); only 1.6 ± 1.1% of the seeds germinated in the dark. There was a marginally significant response to stratification (light *vs* stratification MS = 450.00, $F_{1,3} = 3.27$, $P = 0.0955$). After chilling, 67.5 ± 20.0% of viable seeds germinated. The after-ripening treatment appeared to induce dormancy (light *vs* after-ripening MS = 935.28, $F_{1,3} = 6.80$, $P = 0.0229$; Fig. 1). Results of the GLM are shown in Table 3.

As with *A. menziesii* var. *intermedia*, it was only in the light treatment that germination continued to increase after the first week. The germination percentage in this treatment went from 9.4 ± 5.1% after 1 week to 39.1 ± 13.8% after 4 weeks (Fig. 2).

Blepharipappus scaber This species was highly dormant after 9 months of dry storage; there was no germination in either the light or dark treatments. Four weeks of cold stratification broke dormancy for a small (20.1 ± 4.4), but significant (light *vs* stratification MS = 2926.13, $F_{1,3} = 295.69$, $P < 0.0001$) percentage of the seeds. None of the treatments applied allowed for more than 20% of viable seeds to germinate (Fig. 1). Results of the GLM are shown in Table 3.

For this species, germination did not increase from week one through to week four in any treatment (Fig. 2).

Descurainia pinnata This species had very low dormancy levels after 12 months of dry storage. In contrast to the other species, germination was higher in the dark (98.2 ± 3.7%) than in the light treatment (62.5 ± 24.0%; MS = 1937.53, $F_{1,3} = 12.83$, $P = 0.0038$; Fig. 1). Neither stratification nor after-ripening had a significant effect on

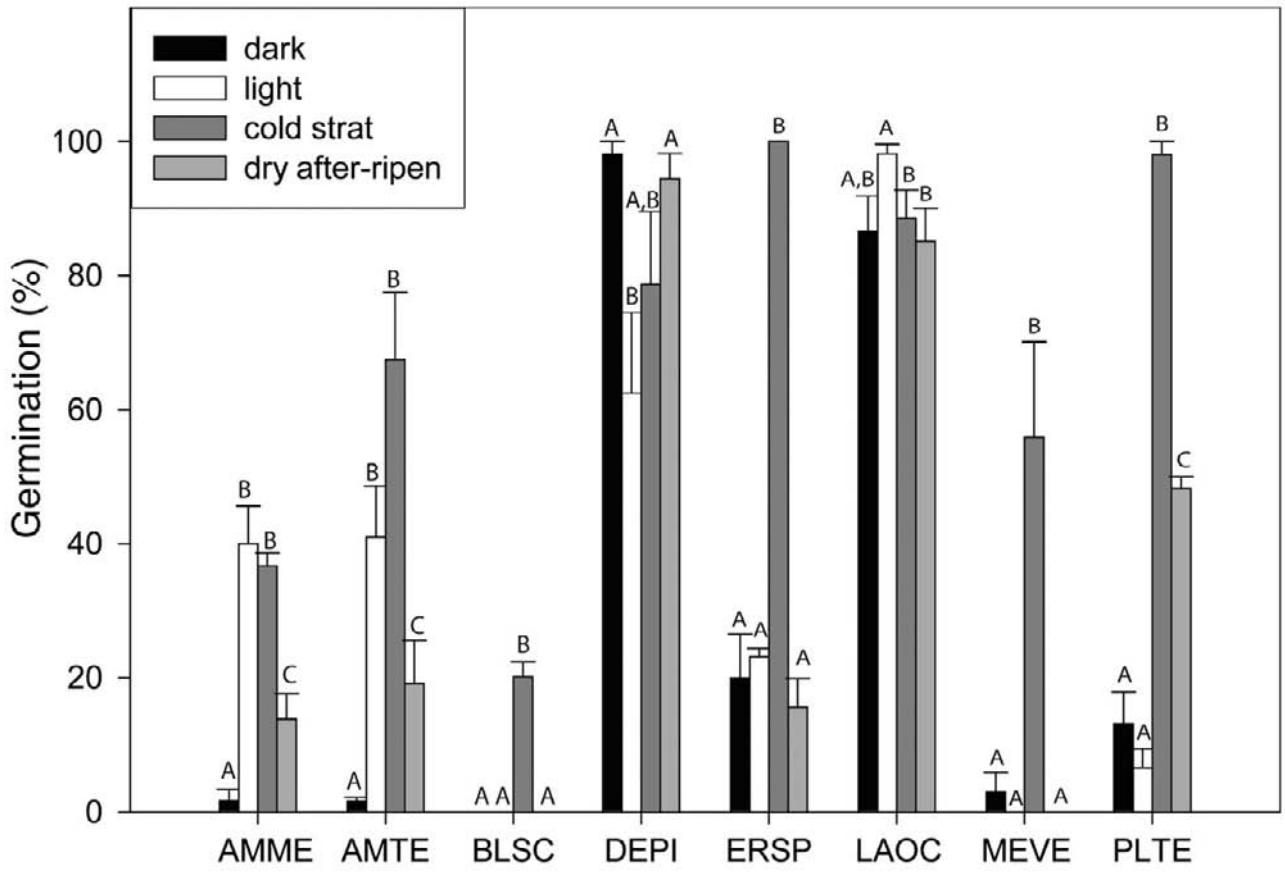

Fig. 1 Percentage germination under each of four treatments: light constant temperature, dark constant temperature, cold stratification (cold strat) and hot, dry after-ripening (dry after-ripen). Error bars represent one standard deviation. The letters represent differences among least square (LS) means using a Bonferroni adjustment for multiple comparisons. All comparisons among treatments were done by species. AMME, *Amsinckia menziesii* var. *intermedia*; AMTE, *Amsinckia tesselata*; BLSC, *Blepharipappus scaber*; DEPI, *Descurainia pinnata*; ERSP, *Eriastrum sparsiflorum*; LAOC, *Lappula occidentalis*; MEVE, *Mentzelia veatchiana*; PLTE, *Plagiobothrys tenellus*.

Table 3 Results of the general linear model of treatment effects on germination percentage after 4 weeks

Species	Source	MS	*F*	*P*
Amsinckia menziesii var. *intermedia*	Treatment	2539.77	37.88	< 0.0001
Amsinckia tesselata	Treatment	2910.31	21.17	< 0.0001
Blepharipappus scaber	Treatment	1463.06	147.85	< 0.0001
Descurainia pinnata	Treatment	747.56	4.95	< 0.0183
Eriastrum sparsiflorum	Treatment	4949.08	57.05	< 0.0001
Lappula occidentalis	Treatment	234.77	3.08	0.0682
Mentzelia veatchiana	Treatment	4550.89	32.37	< 0.0001
Plagiobothrys tenellus	Treatment	5605.35	50.16	< 0.0001

All results based on Type III SS. Pre-planned independent contrast comparisons among treatments appear in Figure 1.

dormancy levels relative to the dark treatment (Fig. 1). Results of the GLM are shown in Table 3.

Germination in week one was relatively high for two of the four treatments, the dark and stratification treatments. In the other two treatments, germination increased substantially after the first week. For the light treatment, germination increased from 19.7 ± 18.7% in week one to 62.5 ± 24.1% in week four. In the after-ripening treatment, it went from 22.0 ± 5.8% in week one to 94.9 ± 8.0% in week four (Fig. 2).

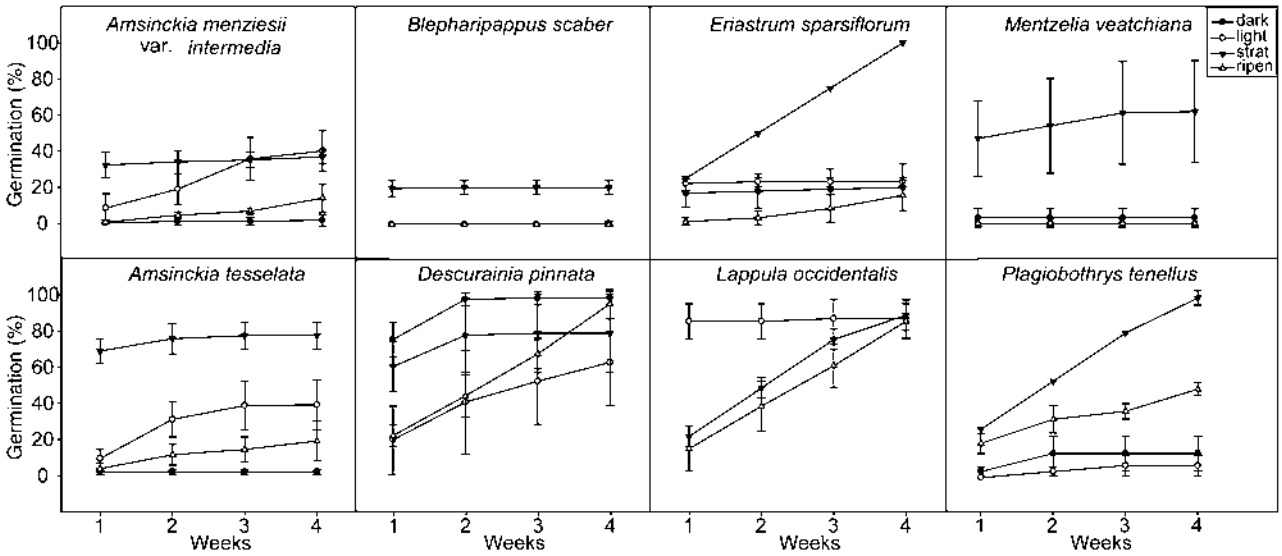

Fig. 2 Germination rate curves by species and treatment. Symbols represent mean cumulative germination percentages. Error bars represent one standard deviation. All values are adjusted using viability data. Strat, stratification; ripen, dry after-ripening, light and dark are the original dormancy test conditions. These data are presented for comparison purposes and were not analyzed statistically.

Eriastrum sparsiflorum This species was relatively dormant after 12 months of dry storage (23.1 ± 2.5% germination in light; Fig. 1). It showed a strong response to the stratification treatment, with 100% of seeds germinating (light *vs* stratification MS = 8515.13, $F_{1,3} = 98.16$, $P < 0.0001$). The after-ripening treatment did not have a significant effect relative to the light treatment (Fig. 1). Results of the GLM are shown in Table 3.

In this species, germination was below 25% in all treatments in week one, and only increased in the stratification treatment from 25 ± 0% in week one to 100 ± 0% in week four (Fig. 2).

Lappula occidentalis This species was relatively non-dormant and no treatment induced dormancy. After 12 months of dry storage, germination in the light treatment was 98.2 ± 2.8%. Stratification and after-ripening increased dormancy levels slightly (light *vs* stratification MS = 406.13, $F_{1,3} = 5.33$, $P = 0.0395$; light *vs* after-ripening MS = 595.13, $F_{1,3} = 7.81$, $P = 0.0162$; Fig. 1). Results of the GLM are shown in Table 3.

Although all treatments achieved high germination percentages by week four, only the light treatment had high germination in week one. In the other treatments, germination was low in week one, but increased to high levels in week four (e.g. in the stratification treatment germination in week one was 21.3 ± 5.6%, but increased to 88.5 ± 8.5% by week four; Fig. 2).

Mentzelia veatchiana This species had very high levels of dormancy after 9 months of storage. Germination in the light and dark treatments did not differ (Bonferroni $P > 0.05$); germination in the light was 0% and in the dark it was 2.9 ± 5.9%. After-ripening had no effect on dormancy, but stratification broke dormancy in a significant percentage of the seeds (55.9 ± 28.5%; light *vs* stratification MS = 9660.50, $F_{1,3} = 68.71$, $P < 0.0001$). Results of the GLM are shown in Table 3.

The germination percentage in this species did not increase substantially over time in any treatment (Fig. 2).

Plagiobothrys tenellus Dormancy levels were relatively high after 12 months of dry storage. The germination percentage was 6.6 ± 5.6% in the light treatment and did not differ significantly in the dark treatment (MS = 282.03, $F_{1,3} = 2.52$, $P = 0.1381$). Both stratification and after-ripening increased the germination percentage, with stratification resulting in 98.0 ± 4.0% germination, significantly higher (stratification *vs* after-ripening MS = 2610.03, $F_{1,3} = 23.36$, $P = 0.0004$) than the 48.2 ± 3.6% resulting from after-ripening (Fig. 1). Results of the GLM are shown in Table 3.

In *P. tenellus*, germination did not increase substantially after week one in the light or dark treatments. In the cold stratification treatment, germination increased from 26.3 ± 0% in week one to 100 ± 6.6% in week four. A smaller increase was seen over the same period in the after-ripening treatment (Fig. 2).

Fresh seeds dormancy assay

The fresh seeds dormancy assay indicated that many of the studied species have higher dormancy at dispersal than they do after 9 to 12 months of storage. Fresh *A.*

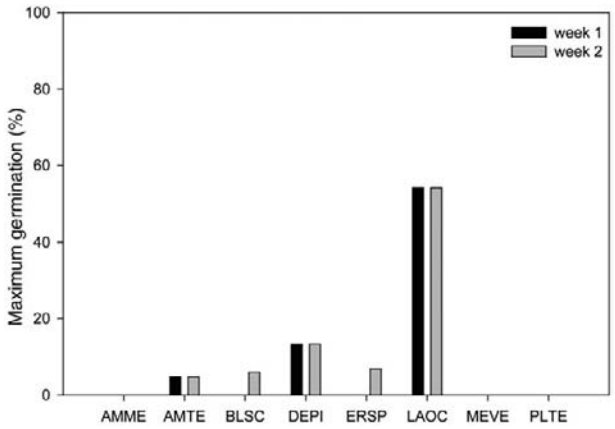

Fig. 3 Maximum percentage germination for fresh seeds, by species, in a 2 week germination check. Symbols represent mean cumulative germination percentages. All values are adjusted using viability data. AMME, *Amsinckia menziesii* var. *intermedia*; AMTE, *Amsinckia tesselata*; BLSC, *Blepharipappus scaber*; DEPI, *Descurainia pinnata*; ERSP, *Eriastrum sparsiflorum*; LAOC, *Lappula occidentalis*; MEVE, *Mentzelia veatchiana*; PLTE, *Plagiobothrys tenellus*.

menziesii var. *intermedia* did not germinate within 2 weeks (Fig. 3; *vs* 18.9% after 2 weeks when seeds had been stored for 9 months; Fig. 2). Fresh *A. tesselata* seeds were relatively dormant, with only 4.8% of viable seeds germinating within 2 weeks (Fig. 3; *vs* 31.1% after storage and then a 2 week assessment under light; Fig. 2). Fresh *D. pinnata* seeds were markedly more dormant at dispersal, with only 13.29% of seeds germinating versus 97.5% in the dark (which had the highest germination percentage at 2 weeks) after storage. Fresh *E. sparsiflorum* seeds were fairly dormant, with only 6.9% germinating after 2 weeks (Fig. 3; *vs* 23.1% after storage and then a 2 week check; Fig. 2.) Fresh *L. occidentalis* seeds germinated at 54.1% of after 2 weeks (Fig. 3; *vs* 97.8% after storage and then a 2 week check.) Fresh *P. tenellus* seeds did not germinate (Fig. 3). In the experiment done after storage, 13.2% germinated in the dark after 2 weeks.

There were two species that did not show markedly higher dormancy when fresh seeds were assayed. Of fresh *B. scaber* seeds, 5.9% germinated after 2 weeks (Fig. 3; *vs* none after storage and then a 2 week germination check; Fig. 2). *Mentzelia veatchiana* seeds were entirely dormant at dispersal, similar to the 3.1% that germinated after storage and a 2 week check.

Discussion

Prediction of germination phenology from laboratory germination data

Winter annuals (facultative and obligate) would be expected to have no requirement for cold stratification (Baskin & Baskin 2001). The species that clearly meet this criterion under the conditions of the present laboratory study are *A. menziesii* var. *intermedia*, *A. tesselata*, *D. pinnata* and *L. occidentalis*. Species that had their highest germination after cold stratification would be expected to be spring germinators, that is, *B. scaber*, *E. sparsiflorum*, *M. veatchiana* and *P. tenellus*.

There is the potential for cyclic dormancy (i.e. seasonal change in dormancy status; Baskin & Baskin 1985; Baskin *et al*. 1993) in species in which dormancy is increased by either stratification or after-ripening. Species in which stratification induces dormancy would be expected to enter dormancy in winter; species in which after-ripening induces dormancy would be expected to enter dormancy in summer. For example, for *A. menziesii* var. *intermedia*, the after-ripening treatment induced dormancy relative to the light treatment.

Differences between stored and fresh seeds

The two *A. msinckias*, *D. pinnata*, *E. sparsiflorum*, *L. occidentalis* and *P. tenellus* appeared to lose dormancy during storage. The fresh seeds dormancy assay was done on different seed lots than the germination experiments, and was not replicated to allow direct statistical comparison, but it provides a qualitative indication that these species do have a dry after-ripening requirement that should result in higher germination percentages following storage than for freshly dispersed seeds. This observation does not change my conclusions about the likely germination phenology of species that have no stratification requirement (*A. menziesii* var. *intermedia*, *A. tesselata*, *D. pinnata* and *L. occidentalis*) or of species that do require stratification (*B. scaber*, *E. sparsiflorum*, *M. veatchiana* and *P. tenellus*). These data also do not change the conclusions about the suitability of these species for use in restoration, as seeds would generally be stored at least from June, when they are dispersed (Tables 1 and 2), through to October or November, when restoration seedings are generally done in the Great Basin (Mazzola *et al*. 2008). However, the lower levels of dormancy of some species after storage versus being freshly dispersed does tell us that species like *D. pinnata* and *L. occidentalis* that had nearly 100% germination without stratification or after-ripening (Fig. 1) germinate at somewhat lower percentages immediately after dispersal (Fig. 2).

Potential for germination niche overlap with cheatgrass

Germination timing can be important in determining competitive interactions (Rice & Dyer 2001), and cheatgrass seeds can germinate extremely quickly once their

dry after-ripening requirements have been met, with most seeds germinating in less than 5 days (Allen *et al*. 1995). Therefore, to effectively compete with cheatgrass, a native annual species would have to germinate rapidly and at high percentages once their requirements are met. For this reason, I decided it would be more informative to look at germination percentages after 1 week than at an index of germination rate (i.e. Timson's index; Timson 1965), which would provide information about overall germination rate. Two of the potential autumn germinators, *D. pinnata* and *L. occidentalis*, germinated to high percentages after a single week without stratification; *D. pinnata* germinated to 75.2 ± 9.5% in the dark and *L. occidentalis* germinated to 98.6 ± 3.7% in the light.

Other considerations for the selection of suitable species for restoration

Germination phenology is an important component of potential success in a restoration seeding; however, there are other considerations in selecting plant materials for restoration or potential competition with cheatgrass. Two of the species that have the potential to germinate in the autumn frequently co-occur with cheatgrass (*A. menziesii* var. *intermedia* and *A. tesselata*). Both *D. pinnata* and *L. occidentalis* occur in disturbed sites, but neither has been observed to occur at high densities with cheatgrass. Such a pattern is difficult to interpret, however, as stands of these species might be excluding cheatgrass, or these species might be experiencing seed limitation in cheatgrass-dominated sites. Two of the species that did not respond as winter annuals in this experimental chamber study also appear to co-occur with cheatgrass (*B. scaber* and *M. veatchiana*), so there appears to be potential for spring annuals to hold their own in a cheatgrass stand.

The behavior of these species in the field may differ. Comparing laboratory results to results from the field will be essential as field results can often be effectively predicted by laboratory experiments (e.g. Meyer & Kitchen 1992), but sometimes show marked differences (e.g. Hendrix 1984).

Seed output is crucial for any species that will be grown commercially. Annual species have a life history that emphasizes reproductive output and should therefore be suitable in this regard. Pilot data on one species (*A. tesselata*) indicate that seed bank density is at least within the range of the overwhelming seed bank density of *B. tectorum* (~26 000 seeds/m^2 for *A. tesselata vs* ~56 000 seeds/m^2 for *B. tectorum*). There is variation among species in the uniformity of timing of seed maturation, both within and among individual plants, and the suitability of individual species' maturation patterns and timing is under pilot investigation by the Great Basin Native Plant Selection and Increase Project. First-year data suggest that at least some species have qualities that would make them suitable for commercial production (S. Jenkins, pers. comm., 2010). Another unknown factor is the relative loss of seeds to seed predators between annual and perennial species, and this is an area for future research.

Cue-non-responsive dormancy and seed bank formation

One species was not induced to germinate at greater than 50% by any of the treatments I applied and this species, *B. scaber*, will require further study. One possible explanation is that this species, as well as the other species that did not achieve 100% germination of viable seeds under any treatment, may have a fraction of the seed population that exhibits cue-non-responsive dormancy to ensure high levels of seed carryover among years (e.g. Meyer *et al*. 2005; Jones 2009). Such 'bet-hedging' is to be expected in annual species, in which the dormant seed is the only life-history stage that is buffered from environmental stochasticity (Doak *et al*. 2002). In fact, long-dormant seeds have been documented in desert annuals (Epling *et al*. 1960; Adonakis & Venable 2004).

I am currently implementing a multi-year seed burial field experiment that will clarify whether these three species have mechanisms to ensure multi-year seed carryover, whether any or all of these species exhibit cyclic dormancy, and what germination phenology looks like in the field. Additional studies examining competitive ability with cheatgrass, both in the greenhouse and in the field, are also being carried out to further evaluate the restoration potential of these species.

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References

Adonakis S. & Venable D. L. (2004) Dormancy and germination in a guild of sonoran desert annuals. *Ecology* **85**: 2582–2590.

Allen P. S., Meyer S. E. & Beckstead J. (1995) Patterns of seed after-ripening in *Bromus tectorum* L. *Journal of Experimental Botany* **46**: 1737–1744.

Association of Official Seed Analysts (1988) Rules for testing seeds. *Journal of Seed Technology* **12**: 1–186.

Baskin J. M. & Baskin C. C. (1973) Delayed germination in seeds of *Phacelia dubia* var. *dubia*. *Canadian Journal of Botany* **51**: 2481–2486.

Baskin C. C. & Baskin J. M. (1983) Germination ecology of *Veronica arvensis*. *The Journal of Ecology* **71**: 57–68.

Baskin C. C. & Baskin J. M. (1985) The annual dormancy cycle in buried weed seeds: a continuum. *BioScience* **35**: 492–498.

Baskin C. C. & Baskin J. M. (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany* **75**: 286–305.

Baskin J. M. & Baskin C. C. (1989) Germination responses of buried seeds of *Capsella bursa-pastoris* exposed to seasonal temperature changes. *Weed Research* **29**: 205–212.

Baskin C. C. & Baskin J. M. (2001) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego.

Baskin J. M., Baskin C. C. & Ehester E. W. (1992) Seed dormancy pattern and seed reserves as adaptations of the endemic winter annual *Lesquerella lescurii* (Brassicaceae) to its floodplain habitat. *Natural Areas Journal* **12**: 84–190.

Baskin C. C., Chesson P. L. & Baskin J. M. (1993) Annual seed dormancy cycles in two desert winter annuals. *Journal of Ecology* **81**: 551–556.

Beckstead J., Meyer S. E. & Allen P. S. (1996) *Bromus tectorum* seed germination: between-population and between-year variation. *Canadian Journal of Botany* **74**: 875–882.

Boutin C. & Harper J. L. (1991) A comparative study of the population dynamics of 5 species of *Veronica* in natural habitats. *Journal of Ecology* **79**: 199–221.

Canals R. M., Eviner V. T., Herman D. J. & Chapin F. S. (2005) Plant colonizers shape early N-dynamics in gopher-mounds. *Plant and Soil* **276**: 327–334.

D'Antonio C. M. & Vitousek P. M. (1992) Biological invasions by exotic grasses, the grass–fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**: 63–87.

DeFalco L. A., Bryla D. R., Smith-Longozo V. & Nowak R. S. (2003) Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* subsp *rubens* (Poaceae) and two native species. *American Journal of Botany* **90**: 1045–1053.

Doak D. F., Thomson D. M. & Jules E. S. (2002) PVA for plants: understanding the demographic consequences of seed banks for population health. In: Beissinger S. R. & McCullough D. R. (eds). *Population Viability Analysis*. University of Chicago Press, Chicago, pp. 312–337.

Epling C., Lewis H. & Ball F. M. (1960) The breeding group and seed storage: a study in population dynamics. *Evolution* **14**: 238–255.

Fargione J., Brown C. S. & Tilman D. (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 8916–8920.

Fowler N. L. (1984) The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in *Linum*. *Journal of Ecology* **72**: 307–318.

Freas K. E. & Kemp P. R. (1983) Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology* **71**: 211–217.

Goergen E. M. & Chambers J. C. (2009) Influence of a native legume on soil N and plant response following prescribed fire in sagebrush steppe. *International Journal of Wildland Fire* **18**: 665–675.

Grime J. P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **11**: 1169–1194.

Haferkamp M. R., Karl M. G. & MacNeil M. D. (1994) Influence of storage, temperature, and light on germination of Japanese brome seed. *Journal of Range Management* **47**: 140–144.

Harper J. L. (1977) *Population Biology of Plants*. Academic Press, Oxford.

Hendrix S. D. (1984) Variation in seed weight and its effects on germination in *Pastinaca sativa* L. (Umbelliferae). *American Journal of Botany* **71**: 795–802.

Humphrey L. D. & Schupp E. W. (2001) Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* **61**: 85–92.

Jones T. A. (2009) Dynamics of dormancy-status subpopulations of Indian ricegrass seed held in dry storage. *Rangeland Ecology and Management* **62**: 284–289.

Kalisz S. & McPeek M. A. (1992) The demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology* **73**: 1082–1093.

Martin A. C. (1946) The comparative internal morphology of seeds. *American Midland Naturalist* **36**: 513–660.

Masuda M. & Washitani I. (1992) Differentiation of spring emerging and autumn emerging ecotypes in *Galium spurium* L. var. *echinospermon*. *Oecologia* **89**: 42–46.

Mazzola M. B., Allcock K. G., Chambers J. C., Blank R. R., Schupp E. W., Doescher P. S. & Nowak R. S. (2008) Effects of nitrogen availability and cheatgrass competition on the establishment of Vavilov Siberian wheatgrass. *Rangeland Ecology and Management* **61**: 475–484.

Meyer S. E. & Kitchen S. G. (1992) Cyclic seed dormancy in the short-lived perennial *Penstemon palmeri*. *Journal of Ecology* **80**: 115–122.

Meyer S. E., Quinney D. & Weaver J. (2005) A life history study of the Snake River Plains endemic *Lepidium papilliferum* (Brassicaceae). *Western North American Naturalist* **65**: 11–23.

Narita K. (1998) Effects of seed release timing on plant life-history and seed production in a population of a desert annual, *Blepharis sindica* (Acanthaceae). *Plant Ecology* **136**: 195–203.

Pellant M., Abbey B. & Karl S. (2004) Restoring the Great Basin desert, U.S.A.; Integrating science, management, and people. *Environmental Monitoring and Assessment* **99**: 169–179.

Rau B. M., Chambers J. C., Blank R. R. & Johnson D. W. (2008) Prescribed fire, soil, and plants: burn effects and interactions in the central Great Basin. *Rangeland Ecology and Management* **61**: 169–181.

Rice K. J. & Dyer A. R. (2001) Seed aging, delayed germination and reduced competitive ability in *Bromus tectorum*. *Plant Ecology* **155**: 237–243.

Roberts H. A. & Neilson J. E. (1982) Seasonal changes in temperature requirements for germination of buried seeds of *Aphanes arvensis*. *L. New Phytologist* **92**: 159–166.

Timson J. (1965) New method of recording germination data. *Nature* **207**: 216–217.

Walck J., Baskin C. C., Hidayati S. N. & Baskin J. M. (2008) Comparison of the seed germination of native and non-native

winter annual Apiaceae in North America, with particular focus on *Cyclospernum leptophyllum* naturalized from South America. *Plant Species Biology* **23**: 33–42.

Whisenant S. G. (1990) Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. In: McArthur E. D. (ed.). *Proceedings for the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management*. Ogden: Gen. Tech. Rep. INT-270. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, pp. 4–10.

Zavaleta E. S. & Hulvey K. B. (2007) Realistic variation in species composition affects grassland production, resource use and invasion resistance. *Plant Ecology* **188**: 139–151.