

Germination patterns of a suite of semiarid grassland forbs from central New Mexico

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ABSTRACT

We examined the germination response of 21 forb species collected from semiarid grasslands of central New Mexico. After-ripened seeds were subjected to 1 of 3 treatments: 1) no treatment; 2) a 3-wk stratification at 5 °C (cold-moist treatment); or 3) a 3-wk warm-moist treatment at 30 °C. All seeds were incubated under an alternating 10/20 °C temperature regime for 6 wk following treatment. Temperature regime had a significant effect on 13 of the 21 species. Twelve species responded positively to the warm-moist treatment, germinating during or following 3 wk at 30 °C. Six species were largely nondormant, germinating under all 3 treatment regimes, and 5 species did not germinate to an appreciable degree under any of the 3 treatment regimes. Ten species responded negatively to the 3-wk stratification, and in only one case was germination slightly improved by the 3-wk stratification. A subsequent 12-wk stratification treatment did, however, increase germination for 3 of the 5 dormant species. These results indicate that, while some species may require stratification, many southwestern grassland forbs are adapted to the combination of moisture and temperature associated with a monsoonal regime, that is, a warm-moist period. Summer, rather than fall, sowing is recommended as it will provide the benefit of dormancy-breaking dry heat followed by warm-moist conditions of the July to September monsoon.

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KEY WORDS

stratification, monsoon, dormancy, restoration

NOMENCLATURE

USDA NRCS (2013)

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CONVERSIONS

5 °C = 41 °F

10 °C = 50 °F

20 °C = 68 °F

30 °C = 86 °F

1 mm = 0.04 in



Figure 1. McKenzie flats, Sevilleta National Wildlife Refuge, is typical of central New Mexico grasslands.

Forbs comprise an under-studied yet important component of vegetative communities, often accounting for the majority of plant species richness (Pokorny and others 2004). They resist the expansion of functionally similar herbaceous weed populations and provide critical habitat and forage needs for pollinators and other wildlife (Shaw and others 2005; Parkinson and others 2013). While early revegetation efforts focused primarily on the use of grass and shrub species, recent native plant and pollinator initiatives (PCA 2013; Pollinator Partnership 2013; USDA Forest Service 2013) have increased the demand for a wide variety of herbaceous flowering plant seeds for use in revegetation seed mixes. As a result, the establishment requirements of forbs have become a research priority (Kitchen 1994; Parkinson and others 2013).

Grasslands of central New Mexico (Figure 1) contain elements of both Chihuahuan Desert scrub and Plains-Mesa grasslands, and are considered to be transitional between the two (Dick-Peddie 1993). Most of the forbs are classified as C₃

and produce flowers and seeds during the spring to early summer before onset of the summer monsoon. Average precipitation is approximately 250 mm, about 60% of which is received during July to September in the form of episodic monsoonal rains (Pennington and Collins 2007). Winter precipitation is highly variable but is generally associated with El Niño years. Meteorological data from the Sevilleta Long Term Ecological Research site (<http://sev.lternet.edu/>) indicate that grasslands in this region are in moisture deficit most of the year, with likely surpluses occurring only during August, December, and January. Although summer monsoonal rains produce the most reliable moisture of the year, winter precipitation results in longer periods of soil moisture that can be utilized in spring as the soil warms (Kemp 1983).

The ecosystem dynamics of semiarid grasslands and transitional Chihuahuan Desert regions of New Mexico have been disrupted by large-scale clearing for agriculture, the introduction of an extensive domestic livestock grazing industry, inva-

sive plants, and increased frequency of insect and disease outbreaks — all leading to a decrease in grassland acreage and biodiversity (Fletcher and Robbie 2004). Successful reestablishment of native vegetation within these grasslands requires an adequate source of site-adapted seeds, as well as knowledge of the component species' germination and establishment requirements. Currently, commercial availability of native seeds, particularly forbs, is inadequate for large-scale restoration of semiarid grassland ecosystems of the Southwest, warranting the development and production of plant materials suitable for restoration on this scale. As a first step toward the development of a native plant materials program for the Southwest, we examined the germination patterns of a number of grassland forbs from central New Mexico. Given the transitional nature of vegetation in central New Mexico, combined with the bimodal moisture pattern, it was expected that germination cues of the various species would reflect patterns associated with both temperate and desert zones.

MATERIALS AND METHODS

We collected seeds of 21 forb species (representing 29 collections) from semiarid grasslands of central New Mexico during the spring and summer of 2006, 2008, and 2010 (Table 1). The majority of seed collections came from the Sevilleta National Wildlife Refuge. The remainder came from grasslands near the towns of Belen and Albuquerque. We stored the seeds in a laboratory at room temperature to allow after-ripening to occur until the start of the experiment. Commercially produced seeds for restoration purposes are similarly after-ripened during warehouse storage prior to their use on the ground. Experiments were conducted from December 2010 to February 2011.

We conducted all germination trials as follows: 2 to 4 replicates of ≥ 25 seeds (depending on availability) were placed in standard 100×15 mm Petri plates on top of 2 circles of blue blotter paper (Anchor Paper Company, St Paul, Minnesota) moistened to saturation with tap water and sealed in plastic bags. We subjected seeds to 1 of 3 treatments: 1) no treatment; 2) a 3-wk stratification at 5°C (cold-moist treatment); or 3) a 3-wk warm-moist treatment at 30°C . The latter 2 temperature regimes simulated winter and summer monsoonal conditions, respectively. All seeds were incubated under an alternating $10/20^\circ\text{C}$ temperature regime for 6 wk following treatment. Previous experiments using constant incubation temperatures had shown 15°C to be optimal for most species (data on file at USDA Forest Service, Rocky Mountain Research Station, Albuquerque, New Mexico). The use of a $10/20^\circ\text{C}$ alternating regime allowed for some diurnal variation in temperature while preserving the optimal mean. Incubation chambers were set at a 12 h light/dark cycle synchronized with the change in temperature. We added tap water to the blotters as needed to maintain moisture during the experiment. Germinated seeds were

counted and removed from the plates 3 times per wk. Seeds were considered germinated if the radicle extended 5 mm or exhibited geotrophic bending. Experiments were terminated following 6 wk at $10/20^\circ\text{C}$, or earlier if germination had ceased. We determined the viability of ungerminated seeds in each plate using the cut test. Seeds that were filled with an intact, white, firm embryo we scored as viable. Germination percentages were adjusted based on the total number of viable seeds.

Five species did not germinate to any appreciable degree (10%) under any of the 3 treatment regimes described above. To see if the 3-wk stratification had been insufficient to break dormancy, we subjected seeds of these 5 species to a 12-wk stratification at 5°C . Four replicates of ≥ 25 seeds per species were prepared as described previously and checked for germination weekly. They were then moved to the $10/20^\circ\text{C}$ incubation temperature for an additional 3 wk and checked for germination thrice weekly.

Treatment effects were analyzed separately for each species. Six of the species had either 2 or 3 collections that varied geographically or temporally. We combined germination results for these species to form additional replicates in the statistical analysis, as germination patterns for each species proved consistent among collections. We ran a fixed-effects logistic regression using SAS PROC LOGISTIC (SAS Institute, Cary, North Carolina) of the final proportion of germinated seedlings on treatment using Firth's penalized likelihood method to alleviate issues with quasi-separation (Firth 1993; Heinze and Schemper 2002). A random effect for "plate" was preliminarily included as part of the model-fitting, but for all species, that effect was either zero or not significantly larger than its own estimated standard error. The random effect was therefore excluded to facilitate estimation across all species. Post hoc comparisons were based on odds ratios. A Tukey-Kramer adjustment was used to adjust *P*-values to properly reflect family-wise Type I error rates.

We also wished to look for groups of species with similar germination patterns. To do this, we performed a complete linkage hierarchical cluster analysis on germination data using Euclidean dissimilarities between the 21 species being clustered. Species were clustered by weekly cumulative germination rates up to 7 wk for each of the 3 treatments. Daily cumulative germination rates were linearly interpolated from periodic but irregularly observed cumulative germination rates. Analyses were performed using R function *hclust* in package *stats* (R Development Core Team 2013).

RESULTS

Treatment had a significant effect on 13 of the 21 species (Table 2). Of the remaining 8 species, 3 maintained dormancy while 5 germinated well regardless of treatment. Two other species, *Mentzelia albicaulis* and *Phacelia integrifolia* (full taxonomic

TABLE 1

Collection year and locations for the 21 species of forbs used in germination study.

Species	Family	Code	Year	Collection location
<i>Allium macropetalum</i> Rydb.	Liliaceae	ALMA4	2010	Sevilleta NWR
<i>A. macropetalum</i>	Liliaceae	ALMA4	2006	Sevilleta NWR
<i>Baileya multiradiata</i> Harv. & A. Gray ex A. Gray	Asteraceae	BAMU	2008	Belen
<i>Calylophus hartwegii</i> (Benth.) P.H. Raven	Onagraceae	CAHA	2006	Sevilleta NWR
<i>Delphinium carolinianum</i> Walter	Ranunculaceae	DECAV2	2006	Sevilleta NWR
<i>Dimorphocarpa wislizeni</i> (Engelm.) Rollins	Brassicaceae	DIWI2	2008	Belen
<i>D. wislizeni</i>	Brassicaceae	DIWI2	2010	Albuquerque
<i>D. wislizeni</i>	Brassicaceae	DIWI2	2010	Sevilleta NWR
<i>Gaillardia pulchella</i> Foug.	Asteraceae	GAPU	2008	Belen
<i>Heliotropium convolvulaceum</i> (Nutt.) A. Gray	Boraginaceae	HECO5	2008	Belen
<i>Ipomopsis laxiflora</i> (J.M. Coulter) V.E. Grant	Polemoniaceae	IPLA2	2006	Sevilleta NWR
<i>Linum puberulum</i> (Engelm.) A. Heller	Linaceae	LIPU4	2006	Sevilleta NWR
<i>Machaeranthera canescens</i> (Pursh) A. Gray	Asteraceae	MACA2	2008	Belen
<i>Machaeranthera pinnatifida</i> (Hook.) Shinners	Asteraceae	MAPIP	2010	Sevilleta NWR
<i>M. pinnatifida</i>	Asteraceae	MAPIP	2010	Albuquerque
<i>M. pinnatifida</i>	Asteraceae	MAPIP	2006	Sevilleta NWR
<i>Malacothrix fendleri</i> A. Gray	Asteraceae	MAFE	2006	Sevilleta NWR
<i>Mentzelia albicaulis</i> (Hook.) Torr. & A. Gray	Loasaceae	MEAL6	2008	Belen
<i>M. albicaulis</i>	Loasaceae	MEAL6	2010	Albuquerque
<i>Nama hispidum</i> A. Gray	Hydrophyllaceae	NAHI	2008	Belen
<i>Oenothera albicaulis</i> Pursh	Onagraceae	OEAL	2010	Sevilleta NWR
<i>O. albicaulis</i>	Onagraceae	OEAL	2006	Sevilleta NWR
<i>Oenothera caespitosa</i> Nutt.	Onagraceae	OECA10	2008	Belen
<i>Penstemon fendleri</i> Torr. & A. Gray	Scrophulariaceae	PEFE	2010	Sevilleta NWR
<i>Phacelia integrifolia</i> Torr.	Hydrophyllaceae	PHIN	2008	Belen
<i>P. integrifolia</i>	Hydrophyllaceae	PHIN	2010	Albuquerque
<i>Plantago patagonica</i> Jacq.	Plantaginaceae	PLPA2	2006	Sevilleta NWR
<i>Townsendia annua</i> Beaman	Asteraceae	TOAN	2006	Sevilleta NWR
<i>Zinnia grandiflora</i> Nutt.	Asteraceae	ZIGR	2006	Sevilleta NWR

nomenclature in Table 1; Figure 2), also remained largely dormant despite small but statistically significant treatment effects. Ten of the 13 species germinated to highest percentages in response to the warm-moist treatment. In contrast, *Machaeranthera pinnatifida* (Figure 3) and *Malacothrix fendleri* exhibited highest germination without treatment. Only *Mentzelia albicaulis* showed a slight increase in germination in response to stratification (9% compared with 3% and 4% for control and the warm-moist treatment, respectively).

Cluster analysis identified 2 major species groups (A and B) and 7 subgroups (# 1 to 7) based on the specificity and pattern of their germination responses (Figure 4). Group A comprised

11 species that exhibited low cumulative germination and (or) responded only to the warm-moist treatment. Nearly all species in this group exhibited low germination rates in response to stratification, the highest being *Malacothrix fendleri* at 13% (Table 2). Two subgroups and 2 individual species occurred within this group. Subgroup #4 consisted of *Dimorphocarpa wislizeni*, *Linum puberulum*, *Heliotropium convolvulaceum*, and *Nama hispidum*. For these species, most of the germination occurred during the warm-moist treatment, with little additional germination during the actual incubation period at 10/20 °C (Figure 6). Subgroup #3 consisted of *Calylophus hartwegii*, *Ipomopsis laxiflora*, *Oenothera albicaulis* (Figure 5),



Figure 2. *Phacelia integrifolia*.



Figure 3. *Machaeranthera pinnatifida*.

Mentzelia albicaulis, and *Phacelia integrifolia*. These 5 species did not germinate to an appreciable degree (10%) following any of the 3 treatments. Thus, new seeds were subjected to a 12-wk stratification at 5 °C, prior to incubation at 10/20 °C. The prolonged chill resulted in partial germination for 3 of the more dormant species: 49% germination for *Mentzelia albicaulis*, 14% for *Phacelia integrifolia*, and 16% for *Ipomopsis laxiflora* (Table 2). Two other species were included in group A. For these 2 species, stratification suppressed germination, but they differed in their response to the other 2 treatments. *Mala-cothrix fendleri* germinated to a large percentage only at 10/20 °C, both treatments inducing dormancy (Figure 3). In contrast, the warm-moist treatment increased germination in *Allium macropetalum* compared with that obtained without treatment (Figure 7).

The second major group (B) consisted of species that germinated to a higher percentage relative to group A and was improved by several treatments. This group included 2 subgroups and a single species (Figure 4). Subgroup #7 comprised *Baileya multiradiata*, *Gaillardia pulchella* (Figure 8), *Oenothera caespitosa*, *Townsendia annua*, *Zinnia grandiflora*, *Machaeranthera pinnatifida*, and *Plantago patagonica*. These species were largely nondormant with most of their seeds germinating rapidly during the warm-moist treatment but also germinating at 10/20 °C to a percentage either similar (*Baileya multiradiata*, *Gaillardia pulchella*, *Zinnia grandiflora*, *Machaeranthera pinnatifida*, *Plantago patagonica*) or lesser (*Oenothera caespitosa*, *Townsendia annua*) (Table 2; Figure 9). *Plantago patagonica* differed from the other 6 species in that the 5 °C stratification treatment induced dormancy. Subgroup #6 consisted of *Penstemon fendleri* and *Delphinium carolinianum*. Both species germinated to a similar percentage regardless of temperature regime (Table 2). *Penstemon fendleri* began germinating during stratification, whereas *Delphinium carolinianum* did not begin germination until removed from stratification (Figure 10). The final species, *Machaeranthera canescens*, was completely nondormant, beginning germination within days of imbibition, even during stratification (Figure 5).

DISCUSSION

Germination research on native plant species has increased dramatically in recent years. A search on native forb seed germination in Google Scholar (<http://scholar.google.com/>) showed a steady yearly increase in the number of journal articles, from 399 in 2000 to more than 1000 in 2012. Research in the western US has focused largely on temperate plant species (for example, Drake and Ewing 1997; Schütz and Rave 1999) and warm desert species, primarily annuals (for example, Freas and Kemp 1983; Clauss and Venable 2000; Adondakis and Venable 2004).

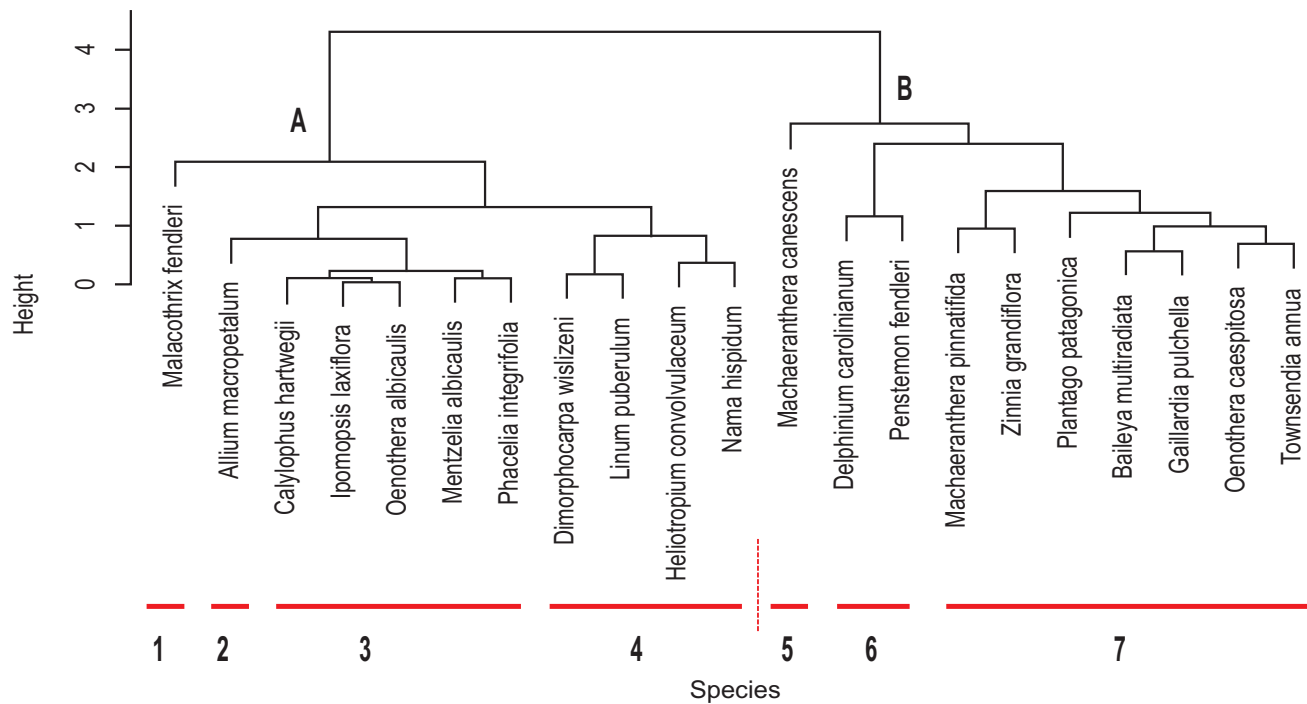


Figure 4. Cluster dendrogram for 21 species of semiarid grassland forbs based on germination response under 3 temperature regimes.

Temperate species, coming from areas with cold and often snowy winters, typically require some degree of stratification to achieve germination (for example, Meyer and Kitchen 1994a; Meyer and Carlson 2004; Scholten and others 2009). Stratification is listed as a requirement for successful germination of a wide variety of temperate plant species (AOSA 2013). In this study, a few species (*Gaillardia pulchella*, *Oenothera caespitosa*, *Penstemon fendleri*, *Machaeranthera canescens*) were able to begin germinating during or following stratification but were also able to germinate to the same or higher levels in other treatments. In only one case, *Mentzelia albicaulis*, did the 3-wk stratification improve germination, and that only marginally. The prolonged 12-wk stratification did result in partial germination for 3 of the more dormant species, indicating a need for a longer exposure to cold conditions, particularly for species of *Mentzelia*. A congener, *Mentzelia veatchiana* Kellogg, required 4 wk of stratification to achieve 56% germination (Forbis 2010). Other New Mexican grassland species, not covered here, may also require stratification for germination.

A second major focus in germination ecology research has been on warm desert species, principally annuals. The annual habit is well-suited to warm desert environments. For example, Evans and others (2005) found that the annual habit of onagraceous species was associated with an increase in summer temperature and a decrease in winter precipitation. Annuals are typically divided into two temporally separated and non-overlapping groups: winter and summer. Winter annuals ger-

minate during the fall through spring and complete their life cycle in spring to early summer, whereas summer annuals germinate during spring to summer and complete their life cycle in autumn. Winter annuals have more stable population dynamics and higher species diversity than do summer annuals (Kemp 1983; Guo and others 2002). The two groups also differ in a number of morphological traits, including height, seed size, growth form, and rooting depth (Mulroy and Rundel 1977; Venable and Brown 1988; Guo and Brown 1997).

Within our study, species forming group A were dominated by winter annuals and exhibited more restricted germination requirements. Because a larger portion of the annual life cycle is delegated to the seed stage, mechanisms that prevent simultaneous germination of all seeds reduce the probability of extinction (Freas and Kemp 1983). The buildup of a soil seedbank is considered to be a type of bet hedging—increased long-term population mean fitness through a reduction in the year-to-year variation, at the expense of fitness in any given year (Cohen 1966; Evans and others 2007; Venable 2007). Within our study, only a portion of seeds in subgroup #4 germinated, responding only to the warm-moist treatment (Figure 3). Seeds that did not germinate may enter secondary dormancy in response to winter chill, with another fraction germinating in early spring (Baskin and Baskin 1998). Support for this scenario comes from Kemp (1983), who reported both early August and mid-March germination for *Linum vernale* Woot., a close relative of *Linum puberulum*. Cycles of dormancy/nondormancy have been reported

TABLE 2

Germination percentages of after-ripened seeds of 21 species following 1 of 3 treatments.

Subgroup/species	10/20 °C	3-wk Treatment		Chi-square P-value	12-wk Stratification
		5 °C	30 °C		
Subgroup #1					
<i>Malacothrix fendleri</i>	66 a	13 b	15 b	0.0001	—
Subgroup #2					
<i>Allium macropetalum</i>	24 b	8 c	50 a	<0.0001	—
Subgroup #3					
<i>Calylophus hartwegii</i>	1	1	1	ns	0
<i>Ipomopsis laxiflora</i>	5	2	3	ns	16
<i>Oenothera albicaulis</i>	4	4	4	ns	4
<i>Mentzelia albicaulis</i>	3 b	9 a	4 b	<0.0001	49
<i>Phacelia integrifolia</i>	4 b	8 a	8 a	0.0147	14
Subgroup #4					
<i>Dimorphocarpa wislizeni</i>	5 b	0 c	54 a	<0.0001	—
<i>Linum puberulum</i>	0 b	0 b	58 a	<0.0001	—
<i>Heliotropium convolvulaceum</i>	1 b	4 b	34 a	<0.0001	—
<i>Nama hispidum</i>	7 b	4 c	22 a	<0.0001	—
Subgroup #5					
<i>Machaeranthera canescens</i>	100	99	100	ns	—
Subgroup #6					
<i>Delphinium carolinianum</i>	84	79	100	ns	—
<i>Penstemon fendleri</i>	100	96	95	ns	—
Subgroup #7					
<i>Machaeranthera pinnatifida</i>	96 a	63 c	91 b	<0.0001	—
<i>Zinnia grandiflora</i>	97	87	91	ns	—
<i>Plantago patagonica</i>	76 a	7 b	67 a	<0.0001	—
<i>Baileya multiradiata</i>	59	67	72	ns	—
<i>Gaillardia pulchella</i>	77 a	65 b	86 a	0.0015	—
<i>Oenothera caespitosa</i>	47 b	29 c	93 a	<0.0001	—
<i>Townsendia annua</i>	72 b	47 c	93 a	<0.0001	—

Notes: Treatments: 1) no treatment; 2) a 3-wk stratification (5 °C for 21 d); or 3) a 3-wk moist-warm treatment (30 °C for 21 d). All seeds were then incubated at an alternating 12-h diurnal regime of 10/20 °C. Germination percentages were adjusted by total viability for each collection. Treatment percentages followed by different letters within a species are significantly different at $P \leq 0.05$. Seeds exhibiting exceptionally low germination under the 3 treatment regimes were subsequently subject to an additional 12-wk stratification (5 °C for 84 d), followed by incubation for 3 wk at 10/20 °C. These long-term stratification data were not included in the statistical analyses.



Figure 5. A field of *Oenothera albicaulis*.

for a number of winter annuals, as well as for short-lived perennials (Freas and Kemp 1983; Kitchen and Meyer 1992; Baskin and others 1993).

Models of bet hedging predict that the greater the variation in environmental conditions associated with germination, the smaller the fraction of seeds germinating at any one time (Ellner 1985). In that regard, note that *Dimorphocarpa wislizeni* (Figure 11) and *Linum puberulum*, which germinated to 54% and 58%, respectively, reportedly emerge much earlier in the

spring when conditions are more stable than do *Heliotropium convulvulaceum* and *Nama hispidum*, which germinated to 34% and 22%, respectively (Kemp 1983). *Malacothrix fendleri* differed from the 4 species in subgroup #4 in that both stratification and a warm-moist treatment induced dormancy. *In situ*, *Malacothrix fendleri* germination would likely occur only in the spring after soils warmed up, with ungerminated seeds remaining in the seedbank.

Two perennials, *Allium macropetalum* and *Calylophus hartwegii*, also clustered with the annuals of group A. Members of the genus *Allium* have deep simple morphophysiological dormancy, with underdeveloped embryos (Martin 1946; Baskin and Baskin 1998). Physiological dormancy is broken at high temperatures, followed by embryo development and germination in cooler moist conditions of autumn or spring (Baskin and Baskin 1998). In this study, some germination of *Allium macropetalum* occurred without warm-moist treatments; however, seeds likely experienced dry heat prior to collection that may have broken physiological dormancy. Germination only occurred under the cooler 10/20 °C regime, which corresponds with the finding of Kemp (1983) who reported emergence of *Allium macropetalum* in mid-March.

Several species in group A, including *Calylophus hartwegii* and *Oenothera albicaulis*, exhibited only minimal germination regardless of temperature regime. These species require further investigation of their germination requirements. In that effort, a number of other treatments have been proposed, including smoke, dry heat, darkness, and wet/dry cycles. For example, *Phacelia tanacetifolia* Benth. seeds are inhibited by light (Chen and Thimann 1966), and seeds of some species of *Gilia* Ruiz &

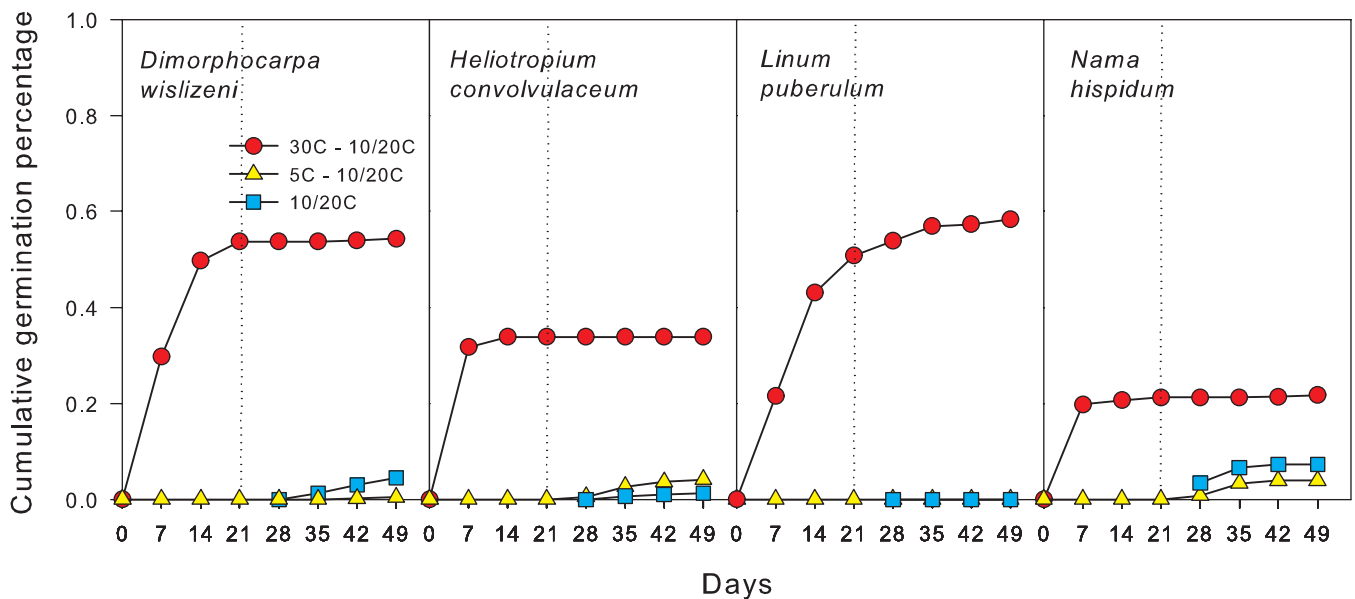


Figure 6. Cumulative germination percentages for the 4 species of subgroup #4 under 3 temperature regimes. Dotted line marks removal of germination plates from stratification and warm-moist treatments to the 10/20 °C incubation temperature.

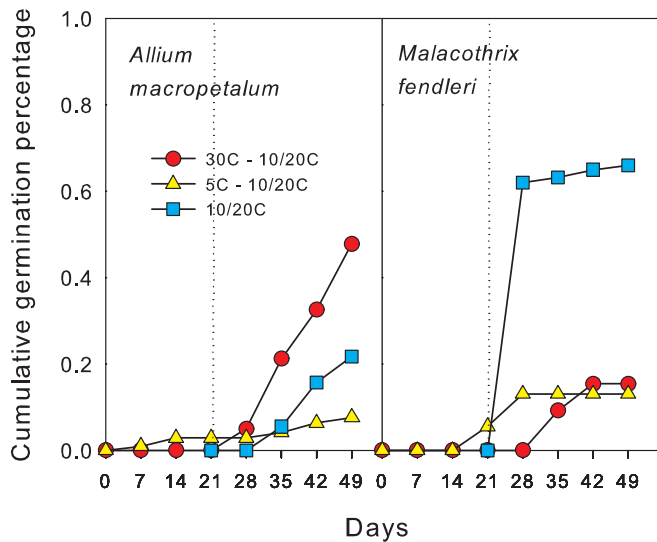


Figure 7. Cumulative germination percentages for the 2 species comprising subgroups #1 and #2 under 3 temperature regimes. Dotted line marks removal of germination plates from stratification and warm-moist treatments to the 10/20 °C incubation temperature.

Pav. (Polemoniaceae) are stimulated by dry heat and (or) charred wood (Baskin and Baskin 1998).

Group B consisted largely of perennials that flower in spring or early summer. Perennials have multiple chances to reproduce, thereby increasing the likelihood of their seeds experiencing a good recruitment year and decreasing the probability of extinction compared with annuals. Germination percentages for this group were close to 100% for most species and, with the exception of *Plantago patagonica*, some germination occurred under all treatment regimes. Species in subgroup #7



Figure 8. *Gaillardia pulchella*.

(Figure 4) are all capable of germinating during warm wet monsoonal conditions, as well as in cooler autumn conditions. Four of these species are composites (*Baileya multiradiata*, *Gaillardia pulchella*, *Zinnia grandiflora*, and *Machaeranthera pinnatifida*). Baskin and others (1994) examined germination requirements of 6 perennial spring-maturing species of warm desert composites, including a species of *Gaillardia*. For those 6 composites, warm summer temperatures decreased dormancy, followed by germination under cooler fall temperatures. This germination behavior was similar to that exhibited by subgroup #6, in which *Delphinium carolinianum* and *Penstemon fendleri* germinated at 10/20 °C, which corresponds to cooler fall or spring conditions.

Two annuals, *Townsendia annua* and *Plantago patagonica*, clustered with the perennials of group B. Stratification reduced germination percentages for these 2 species, as well as for *Oenothera caespitosa*. *Plantago patagonica*, in particular, exhibited secondary dormancy following stratification at 5 °C, responding in a manner similar to that of the annual species comprising subgroup #4. Also, similar to species in subgroup #4, *Plantago patagonica* germinated only a fraction of its seeds in response to either warm monsoonal conditions or fall and spring conditions. Several other species in subgroup #7 are likely to have some ability to form a seedbank. Short-lived arid-land perennials can have germination patterns similar to those of annuals (Kitchen and Meyer 1992), and bet hedging has been reported to occur in desert perennial species (Evans and others 2007).

Machaeranthera canescens did not exhibit dormancy in this study (Figure 5), although dormancy may have been broken by summer heat prior to collection or through after-ripening in the laboratory. A plant guide for *Machaeranthera canescens*, published by the USDA Natural Resources Conservation Service (Tilley and others 2010), indicates the need for stratification. This recommendation was, however, based on a propagation protocol in which all of the seeds were stratified (Parkinson and DeBolt 2005). While our collection did not require stratification, the seeds were collected from a single location. Seed germination behavior can differ widely within species as a result of geographic and climatic differences among seed collection locations (Meyer and Kitchen 1994a, 1994b; Pendleton and Meyer 2004).

CONCLUSION

Much of the recent restoration work on western US rangelands has focused on the Intermountain region and northern plains in response to wildfire, invasive species, oil and gas extraction, and restoration of sage grouse habitat (GBNPSIP 2013; GBRI 2013; JFSP 2013; SageSTEP 2013). Fall seeding is generally preferred, as many species currently used in restoration require stratification for germination. Our results indicate that, while

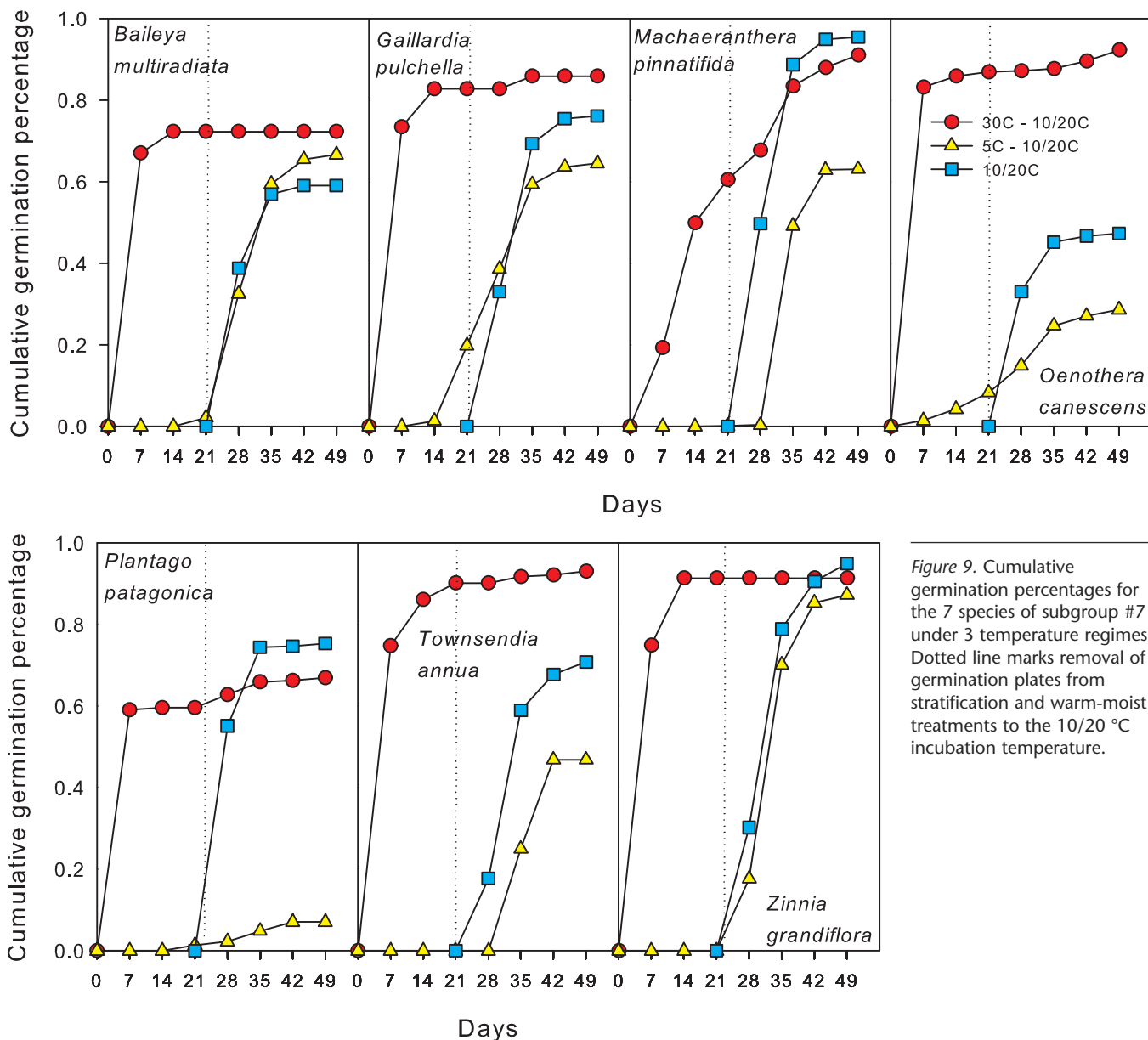


Figure 9. Cumulative germination percentages for the 7 species of subgroup #7 under 3 temperature regimes. Dotted line marks removal of germination plates from stratification and warm-moist treatments to the 10/20 °C incubation temperature.

some species may require stratification, many southwestern grassland forbs, especially annuals, are adapted to the combination of moisture and temperature associated with a monsoonal regime. Seeds collected from these areas would benefit from summer sowing, rather than fall, to benefit from dormancy-breaking heat and moist warm conditions provided by the July to September monsoon. Future field tests of germination and emergence phenology, however, are needed to confirm these laboratory results. Climate change scenarios suggest northern range expansion for many vegetation types, including semiarid grasslands (Rehfeldt and others 2006; Archer and Predick 2008). Information on germination patterns across the geographic and elevational range of potential restoration species is important for the conservation, restoration, and maintenance of functional grassland ecosystems.

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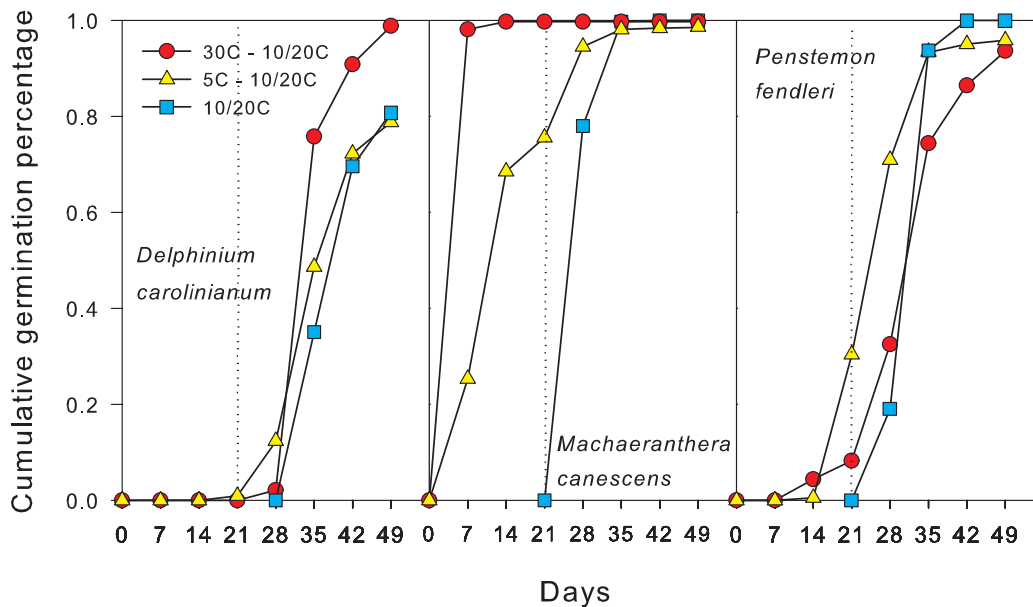


Figure 10. Cumulative germination percentages for the 3 species comprising subgroups #1 and #2 under 3 temperature regimes. Dotted line marks removal of germination plates from stratification and warm-moist treatments to the 10/20 °C incubation temperature.

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Figure 11. *Dimorphocarpa wislizeni*.

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