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Germination Response of Prairie Dropseed and Hairy Goldaster to Stratification and Temperature

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ABSTRACT The unique vegetation assemblage of the Black Hills in conjunction with the frequent occurrence of natural and anthropogenic disturbances emphasizes the need to use locally adapted native species in a wide variety of restoration efforts. However, a general lack of information regarding germination and propagation requirements for most native plant species has restricted their usage. A better understanding of dormancy and germination patterns for native species will increase their availability and affordability. We selected two common native species, hairy goldaster (*Heterotheca villosa*) and prairie dropseed (*Sporobolus heterolepis*), to determine their optimum germination conditions. We hand harvested seeds during 2007–2009 for use in germination trials following two pre-treatment conditions (2-week stratification at 5° C and no stratification), under seven temperature treatments in 2009. We used tetrazolium (2, 3, 5-triphenyl-2H-tetrazolium chloride) to determine germination potential of ungerminated seeds. Recognizing significant treatment interactions for both species, percent germination of hairy goldaster seeds was greatest under cooler constant temperatures (15° C or 20° C) with no stratification. Germination of prairie dropseed seeds was significantly influenced by the year in which seeds were collected, which also determined how the seeds responded to stratification. For both species, stratification significantly increased germination of at least one extreme of the temperature gradient (15° C or 30° C). Patterns of germination observed for both are consistent for species inhabiting grasslands and meadows with a fluctuating environment and subjected to moderate seasonal disturbances.

KEY WORDS Black Hills, germination, Hairy goldaster, Prairie dropseed, stratification treatment, temperature treatment

The Black Hills of South Dakota is an intensively managed area and has been for more than a century (Ball and Schaefer 2000). Most management activities in the Black Hills National Forest are primarily concerned with timber production (Ball and Schaefer 2000); however, management plans also include consideration for wildlife habitat, rangeland improvement, fire fuels reduction, recreation activities, and control of pests, disease, and invasive species (Shepperd and Battaglia 2002). Such management activities can profoundly impact plant communities in the Black Hills. In a recent vegetation survey, Marriott et al. (1999) found that 28 of 68 classified plant communities in the Black Hills were considered globally rare (G1–G3). The unique vegetation assemblage in conjunction with the frequent occurrence of natural and anthropogenic disturbances in the Black Hills emphasizes the need for locally adapted species that can be used in a wide variety of restoration efforts. However, a general lack of information regarding germination and propagation requirements for most native plant species has inhibited their availability and usage.

We selected prairie dropseed (*Sporobolus heterolepis*) and hairy goldaster (*Heterotheca villosa*) for this study because of their widespread distribution throughout a wide variety of plant communities in the Black Hills (Larson and Johnson 1999). Prairie dropseed is a warm-season, tufted, native, perennial grass that is widely distributed throughout the United States and Canada, especially in the Great Plains where it is considered characteristic of a variety of tall- and mixed-grass plant communities (NatureServe 2011). In the Black Hills, it is an indicator species for the high elevation, endemic montane grasslands that are currently listed as globally- and state-imperiled (G1S1) by the Natural Heritage Network and The Nature Conservancy (Marriott et al. 1999, NatureServe 2011). The seeds of prairie dropseed are relatively large; however, we found no published documentation of seed herbivory. This species also was used in landscaping as a native ornamental (Springer 2001).

Hairy goldaster is a perennial forb of the Asteraceae that is distributed throughout the United States from Michigan to the West Coast and from North Dakota to Texas (United States Department of Agriculture 2009). Although it is predominantly found in the western United States, its native range also includes portions of Canada. It is widely used as an ornamental and has been listed as a forage species for bighorn sheep in Nebraska (Vardiman 2010).

Guidelines governing the germination requirements of prairie dropseed and hairy goldaster have yet to be established. For many plant species, especially native species, cold-moist stratification and alternating temperature regimes often enhance seed germination. Temperature requirements for dormancy-breaking and germination

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initiation can provide an indication of the intrinsic environmental conditions from which a seed was derived, yet identifying and satisfying those conditions has proven challenging for many seed researchers. Our objectives were to use hand-collected seeds from diverse, wild populations in the Black Hills to 1) evaluate germination under different temperature regimes, 2) examine the effects of cold-moist stratification on the response of seed germination to temperature, and 3) evaluate the year to year variation in germination. Such information is important in identifying the optimal environmental conditions to overcome dormancy and induce germination with the ultimate goal of increasing the availability, usability, and affordability of these species for restoration projects and promoting the use of locally adapted native species in landscaping.

STUDY AREA

The Black Hills comprised an unglaciated, mountainous uplift that spanned approximately 200 km north to south and 100 km east to west, covering an area of about 15,540 km^2 (Froiland 1990). Elevation ranged from 914 m in low-lying areas to 2,208 m at the highest point (Harney Peak). The climate of the Black Hills and surrounding Northern Great Plains was representative of the temperate steppe, which was characterized by cold winters and hot summers (Bailey et al. 1994). Average annual precipitation in the Black Hills from 1971–2000 ranged from 51 cm in the southern region to 76 cm in the northern region. The temperature minimum/maximum in the northern Black Hills (Lead, SD) averaged –10° C/0° C in January and 13° C/25° C in July; while the minimum/maximum in the southern region (Custer, SD) averaged –11° C/2° C in January and 11° C/27° C in July (South Dakota Office of Climatology 2010). Length of the growing season varied by elevation and latitude but typically comprised 100–154 days between May and September (Heyward 1928, Shepperd and Battaglia 2002).

Vegetation of the Black Hills was a culmination of species overlap from Cordilleran Forest, Grassland, Eastern Deciduous Forest and Northern Coniferous Forest biomes (Marriott et al. 1999). Vegetation classifications of the Black Hills tended to center around Ponderosa pine (*Pinus ponderosa*) because of its role as a dominant species that was only absent from areas that were characteristically treeless (Hoffman and Alexander 1987). Hoffman and Alexander's (1987) habitat type classification recognized eight habitat types for ponderosa pine and included additional habitat classifications for areas dominated by bur oak (*Quercus macrocarpa*), quaking aspen (*Populus tremuloides*), and Black Hills spruce (*Picea glauca*). Plant community classification by Marriott et al. (1999) followed the U.S. National Vegetation Classification System which resulted in 68 plant associations for the Black Hills area; fifteen of the 68 were dominated by ponderosa pine. Both species selected for this study were reported among several of the 68 plant associations described by Marriot et al. (1999). Four of the 28 globally rare plant associations found in the Black Hills contained at least one of the species. Prairie dropseed was recorded among seven total plant associations, three of which were considered rare. Hairy goldaster was found among 11 total plant associations, three of them rare.

METHODS

We hand-collected seeds for this study from 7 sites located within the central to west-central portions of the Black Hills during the summers of 2007–2009 from mid-August through mid-September when the seed units were mature and ready to be shed. For hairy goldaster, we collected seeds when the pappus on the achenes was evident, while prairie dropseed seeds were collected when the florets began disarticulating from the spikelets. The distance between collection sites ranged from 5 km to 39 km (average distance = 21 km, SD = 9.2) based on 21 straight-line measurements between sites. Each collection year represented a 'seed lot' (i.e. 2007 seed lot, 2008 seed lot, and 2009 seed lot). Cleaned seeds were stored dry at –12° C to maintain viability (Walters et al. 2005). In January 2009, we randomly selected filled seeds for evaluating initial viability prior to the germination trials.

We tested the initial viability of collected seeds using standardized tetralozium (TZ) tests (Peters 2000). Two hundred randomly selected seeds of each species were first imbibed with distilled water and soaked for 4 hours (hairy goldaster) or 12 hours (prairie dropseed) in a 1.0% concentration of 2, 3, 5-triphenyl-2H-tetrazolium chloride solution. Hydrogen ions, produced by cellular respiration of living tissue, combined with Tetrazolium to form an insoluble red formazan dye (Cottrell 1947, Lambou 1953, Baskin and Baskin 1998). The result was a red stain of living tissue that indicated viability in both dormant and non-dormant seeds (Baskin and Baskin 1998).

After the initial viability was determined, we conducted germination trials for each seed lot under two pre-treatment conditions (stratified and non-stratified) and seven temperature treatments. We applied the stratification treatment for two weeks on three layers of moistened blotter paper at 5° C. Baskin and Baskin (1998) point out that there are few studies that investigate the optimal cold stratification interval for temperate grassland species; however, of the available studies, the requisite period appeared to be brief. Additionally, Totterdell and Roberts (1979) and Bouwmeester and Karssen (1992) found that dormancy can be re-induced through extended stratification periods.

We placed 50 randomly selected filled seeds from each collection year in 12-cm × 12-cm plastic germination boxes on double-layer blotter paper. We randomly assigned each germination box (our experimental unit) to a stratification and temperature treatment combination and each treatment combination (seed lot, stratification, and temperature) was replicated 8 times. We transferred the germination boxes to one of the seven temperature treatments that consisted of three alternating temperature settings (15/25° C, 15/30° C, and 20/30° C) and four constant temperatures (15° C, 20° C, 25° C, and 30° C) controlled within ± 1° C. During one 24-hour period, each of the temperature treatments was provided 8 hrs of light and 16 hrs of darkness. The alternating temperature cycles incorporated the light period during the highest temperature interval. We conducted germination counts at 28 days, at which time we terminated the germination experiment. We evaluated prairie dropseed germination based on the presence of an elongated coleoptile with enclosed leaves, an attached endosperm, and an elongated primary root. Seed germination for hairy goldaster was based on the presence of an elongated primary root and secondary root structures, an elongated hypocotyl, and photosynthetically active cotyledons. All of these seedling characteristics indicate the ability to produce and sustain a functional plant (Association of Official Seed Analysts 2007). At the conclusion of the germination trials, we tested the viability of ungerminated seeds using standardized tetralozium (TZ) tests as described above.

We calculated dormancy by dividing the number of ungerminated viable seeds, detected using the TZ test, after 28 days by the total number of ungerminated seeds. Because of the non-random nature of the dormancy data, only descriptive statistics (mean ± 95% confidence intervals) were calculated. We analyzed the effects of temperature, stratification, and seed lot (2007, 2008, and 2009), and their interactions on final germination counts (28 days) using a fixed-effects, generalized linear model for binomially distributed data with the logit link function (SAS Version 9.2; SAS Institute 2008). We separated means using the LS means procedure with a Tukey adjustment to control the experimentwise error rate. For ease of presentation, we separated means among temperature treatments within each stratification treatment (stratified and non-stratified), then across stratification (stratified vs. non-stratified) within individual temperature treatments.

RESULTS

Initial seed viability tests on hairy goldaster seeds that were soaked for 4 hours in TZ solution indicated viability levels (e.g., potential germinability) of 79%, 91%, and 65% for the 2007, 2008, and 2009 seed lots, respectively. Initial TZ tests of the 2007, 2008, and 2009 seed lots for prairie dropseed seeds revealed viability levels of 74%, 99%, and 93%, respectively.

Germination at the end of the experiment was significantly influenced by the interaction of temperature, stratification, and collection year for both species (Table 1). For hairy goldaster, the most dramatic response to temperature occurred at the highest constant temperature treatment (30º C; Fig. 1a). Excluding the constant 30º C temperature treatment, germination under the remaining temperature treatments ranged from 71% to 89% for the 2007 seed lot ($\bar{X}$ = 83%), 71% to 82% for the 2008 seed lot ($\bar{X}$ = 80%), and 85% to 95% for the 2009 seed lot ($\bar{X}$ = 89%). The effect of stratification on germination depended upon seed lot and temperature (Fig. 1b). Excluding the constant 30º C temperature treatment, germination of stratified seeds was either a) similar to their non-stratified counterparts ($P > 0.05$), b) slightly but significantly higher (15/30º C temperature for the 2008 seed lot, ($t_{1,294} = 4.98$, $P < 0.001$), c) or significantly lower ($P < 0.001$), especially for seeds collected in 2007. Germination of stratified seeds exposed to the 30º C temperature treatment was 150% (2007), 184% (2008), and 46% (2009) greater than non-stratified seeds collected the same year and under the same temperature treatment. Final germination following stratification was similar ($P > 0.05$) among seed lots and temperature treatments, including the 30º C temperature (Fig. 1b).

Germination of prairie dropseed seeds was largely influenced by seed lot (Table 1, Fig. 2). Germination of non-stratified seeds (Fig. 2a) collected in 2007 and 2008 was, with the exception of the 15º C temperature ($t_{1,294} = 6.60$, $P < 0.001$), similar ($P > 0.05$) among the temperature treatments and ranged from 21% to 42% (average = 28%), while percent germination of seeds collected in 2009 ranged from 39% to 81% (average = 61%). Germination of non-stratified seeds collected in 2009 averaged 154% and 97% higher than seeds collected in 2007 and 2008, respectively. The effect of temperature on germination was observed mainly in the 2009 seed lot.

Collection year had a major effect on how prairie dropseed seeds responded to the stratification treatment (Fig. 2b). Mean germination of stratified seeds collected in 2007 was similar ($P > 0.05$) to non-stratified seeds across the majority of the temperature treatments, with the 15/25º C temperature treatment serving as the exception ($t_{1,294} = 4.14$, $P = 0.03$). In contrast, mean germination of stratified seeds collected in 2008 was 40% to 100% higher ($P < 0.05$) than their non-stratified counterparts. While germination of non-stratified seeds was similar ($P > 0.05$) between the 2007 and 2008 seed lots, stratification increased germination of the 2008 seed lot compared to the 2007 seed lot at all but the 15º C temperature. There was no effect ($P > 0.05$) of temperature on germination of stratified seeds collected in 2009, again with the exception of the 15º C temperature, however, stratification increased germination at all but the 15º and 20º C temperatures. Average germination of stratified seeds collected in 2009 was 175% and 100% greater than stratified seeds collected in 2007, and 2008, respectively, similar to the trend observed in comparison of non-stratified seeds among seed lots.

Because of the high germination percentages of hairy goldaster seeds, especially at the lower temperatures, there were few ungerminated seeds after 28 days available to evaluate dormancy. Although variable, about 20% of the ungerminated seeds were recorded as dormant, and nearly all of those were observed at the higher temperatures (Fig. 3a). In contrast, overall germination of prairie dropseed seeds was low compared to hairy goldaster seeds. There were few viable seeds in the 2007 seed lot following the 28-day germination trial and most were concentrated at the lower temperatures (Fig. 3b). A similar but more pronounced pattern was observed for the 2008 and 2009 seed lots. Approximately 50% of the ungerminated seeds from the 2008 seed lot under the 15º C temperature were viable, while 75% to 90% of 2009 seed lot under the same temperature were viable, regardless of stratification treatment.

Table 1. Results of the generalized linear model evaluating the effects of temperature (Temp), stratification (Strat), and year of collection (Seed Lot), and their interactions on mean germination percentages for hairy goldaster and prairie dropseed (denominator df = 294) in the Black Hills, South Dakota, during 2007–2009.

		Hairy goldaster		Prairie dropseed	
Effect	df	*F*-value	*P* > *F*	*F*-value	*P* > *F*
Temp	6	209.0	< 0.001	46.1	< 0.001
Strat	1	9.1	0.003	234.5	< 0.001
Temp*Strat	6	54.7	< 0.001	3.4	0.003
Seed Lot	2	127.3	< 0.001	1,067.5	< 0.001
Temp*Seed Lot	12	9.1	< 0.001	22.9	< 0.001
Strat*Seed Lot	2	87.9	< 0.001	95.5	< 0.001
Temp*Strat*Seed Lot	12	17.2	< 0.001	5.8	< 0.001

DISCUSSION

Our findings establish baseline patterns of seed germination for prairie dropseed and hairy goldaster in a laboratory setting where environmental factors were strictly controlled. While dormancy-breaking requirements often are variable and difficult to identify, germination requirements for most seeds typically include adequate moisture levels, suitable temperatures, and proper lighting (Bewley 1997, Finch-Savage and Luebner-Metzger 2006). In addition, interactions among these factors are not well known or understood and may be the result of physiological, nutritional, metabolic, or mechanical properties (Totterdell and Roberts 1979, Bewley and Black 1982). Nonetheless, temperature is often regarded as the single most important environmental factor because of its role in breaking dormancy (Bouwmeester and Karssen 1992, Vleeshouwers et al. 1995) and determining germination success (Baskin and Baskin 1988). While germination was not studied in the field, it is likely that the most productive temperature treatments for both species would correspond to soil temperatures at the time of seedling emergence or, at the very least, to the appropriate season (Washitani and Masuda 1990). Often, lower temperature limitations are a reflection of ecological adaption (ecotype) while upper temperature limits may result from physiological constraints determined by the environment experienced by the parent during seed maturation (Brändel 2006).

While determining germination responses to temperature was complicated by treatment interactions, the overall effect of temperature on germination for hairy goldaster seeds was strongest at a constant temperature of 30º C. This temperature may define the upper metabolic limits for this species with respect to temperature, which appears to be ameliorated by stratification. Stratification has been proven to expedite the dormancy breaking process (Davis 1930, Toole et al. 1955, Baskin and Baskin 1998) and increase the range of temperatures at which seeds can germinate (Baskin and Baskin 1988). In temperate regions of North America, spring and early summer provide environmental conditions that are most conducive to seed germination of most species; therefore, it is reasonable to expect that cold-moist stratification would increase seed germination because it is a simulation of winter conditions. Milberg and Andersson

(1998) suggested that variation in germination within a single seed collection event can be moderated by stratification treatment. This may be the case for stratified seeds exposed to 30º C, which showed higher (*P* < 0.001) germination percentages following stratification for all seed lots.

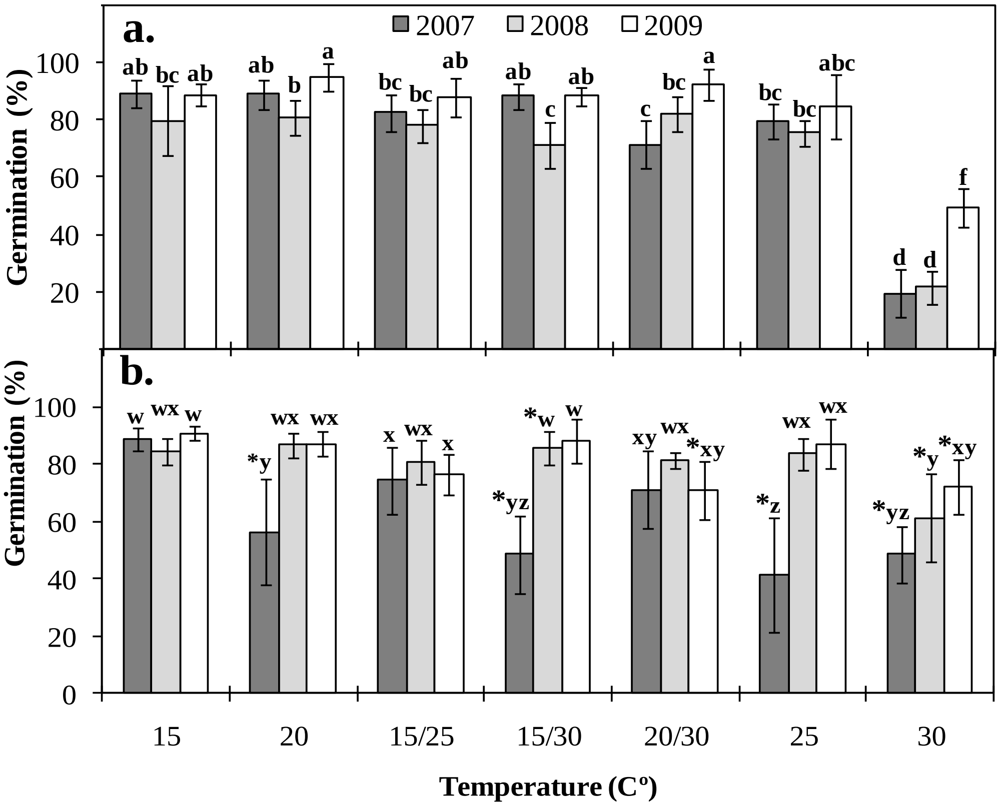

Figure 1. Mean percent germination (± SD) of non-stratified (a) and stratified (b) hairy goldaster (*Heterotheca villosa*) seeds after 28 days in response to temperature treatments. Bars within each graph followed by different letters indicate significant differences (*P* < 0.05) in mean germination (a-f for non-stratified seeds and w-z for stratified seeds). * in lower graph (b) indicates significant differences (*P* < 0.05) in germination percentages between stratified and non-stratified seeds within each temperature treatment.

Effects of stratification and temperature on germination responses of hairy goldaster seeds also were influenced by the year in which seeds were collected. For example, while stratification treatment increased germination of hairy goldaster seeds under high temperature treatments, stratification had a variable effect on other temperature treatments and among seed collection years. For the 2007 seed lot, stratification appeared to increase dormancy in weakly dormant seeds under several temperature treatments (Milberg and Andersson 1998). However, significant variation in germination has been shown to exist between individual plants within a population and between seed collection years that cannot be fully explained by environmental conditions (Andersson and Milberg 1998).

Collection year had a pronounced effect on germination of prairie dropseed seeds while temperature had a relatively minor effect, which suggested more than one optimal temperature similar to results reported by Larson (2002). With one exception (15º C), germination of non-stratified seeds in the 2009 seed lot was greater (*P* <0.001) compared to the 2007 and 2008 seed lots. The observed differences in germination related to collection year may simply be a consequence of the additional time in cold storage for the 2007 and 2008 seed lots, although we found no documentation regarding the longevity of prairie dropseed seeds in cold storage. However, Walters et al. (2005) reported that following 41.8 years of cold storage at –18º C the initial germination of alkali sacaton (*Sporobolus airoides*) was only reduced 13% (96% to 84%). Alternatively, in our study differences in germination responses among years also could be the result of environmental conditions experienced by the parent plant during seed development that influenced the adaptive life histories of the offspring, including patterns of germination (Donohue 2009). Temperature, nutrient, moisture and light availability, light quality, and position held by the seed within the inflorescence or the age of the maternal plant at the time of embryogenesis have been shown to impact seed dormancy and germination (Gutterman 1992). Extreme environmental conditions experienced at the time of seed development, such as high temperatures and water-stress, often result in low seed dormancy and, subsequently, high germination (Allen and Meyer 2002, Figueroa et al. 2010). Conversely, exposure to low temperatures typically results in a prolonged developmental period that allows the seed coat to further develop, which leads to greater seed dormancy (Allen and Meyer 2002, Lacey 1996, Lacey et al. 1997). Seeds for the two species used in our study were collected from a variety of populations. Consequently, the influence of environmental variation on maternal effects was difficult to assess because of the high geographic variation in the Black Hills that influenced temperature and precipitation.

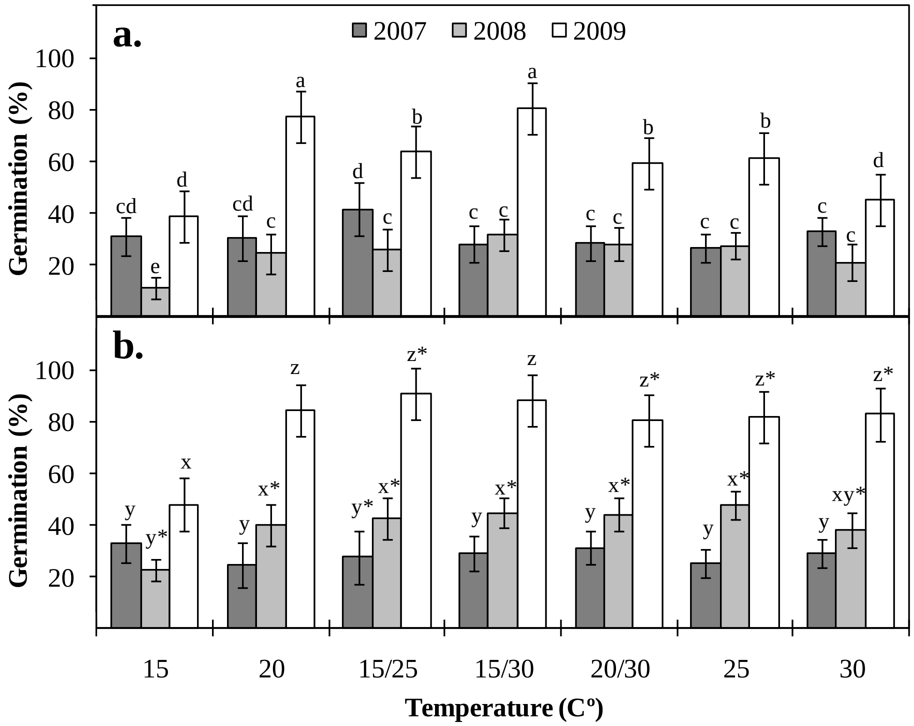

Figure 2. Mean percent germination (± SD) of non-stratified (a) and stratified (b) prairie dropseed (*Sporobolus heterolepis*) seeds after 28 days in response to temperature treatments. Bars within each graph followed by different letters indicate significant differences (P < 0.05) in mean germination (a-f for non-stratified seeds and x-z for stratified seeds). * in lower graph (b) indicates significant differences ($P < 0.05$) in germination percentages between stratified and non-stratified seeds within each temperature treatment.

Interacting effects of temperature, stratification, and seed lot may be further complicated by constant or alternating temperatures, although we did not statistically evaluate the differences in germination among constant and alternating temperatures. We included temperature fluctuations in the experiment because they often signify environmental changes that are essential for seed germination, such as soil depth, seasonality, and niche availability (Grime 1979, Baskin and Baskin 1988, Van Assche and Vanlerberghe 1989). More extreme differences (greater amplitude) in temperature fluctuations naturally signify the arrival of spring and early summer, while soil temperatures stabilize as summer progresses. Likewise, seeds at varying soil depths gauge burial depth by the amplitude of temperature fluctuations, which is less at greater soil depths and more pronounced at the surface. The presence and extent of openings in vegetative cover also are conveyed through temperature fluctuations because vegetation acts as an insulator that stabilizes ground surface temperatures (Pearson et al. 2002). Overall, we did not observe any detectable germination responses to alternating temperatures for either species. However, determining effects of alternating temperatures often are complicated by at least nine related factors that include amplitude, number of cycles, warming rate, cooling rate, higher temperature value, lower temperature value, length of interval at the higher temperature, length of interval at the lower temperature, and the timing of cycle(s) after imbibition (Totterdell and Roberts 1980).

Dormancy of all ungerminated seeds was evaluated at the end of the experiment (Fig. 3). The few ungerminated hairy goldaster seeds determined to be dormant were typically those seeds under the higher temperatures with no apparent trend with respect to stratification or seed lot. In general, the percent of total live seed (germinated plus dormant) was equal to or greater than the percent of viable seeds evaluated prior to germination trials. Notable exceptions were the stratified and non-stratified seeds exposed to the 30º C temperature treatments that were collected in 2007 and 2008. In contrast, the percent of dormant seeds at the end of the experiment for prairie dropseed appeared to be influenced by seed lot and temperature, suggesting considerable loss of seed viability at the higher temperatures, there was no obvious effect of stratification. Thus, total live seeds for prairie dropseed were substantially less than the initial viability values for the majority of the treatment combinations. In this case, the exceptions were seeds collected in 2009 exposed to the lower temperatures (<15/30º C).

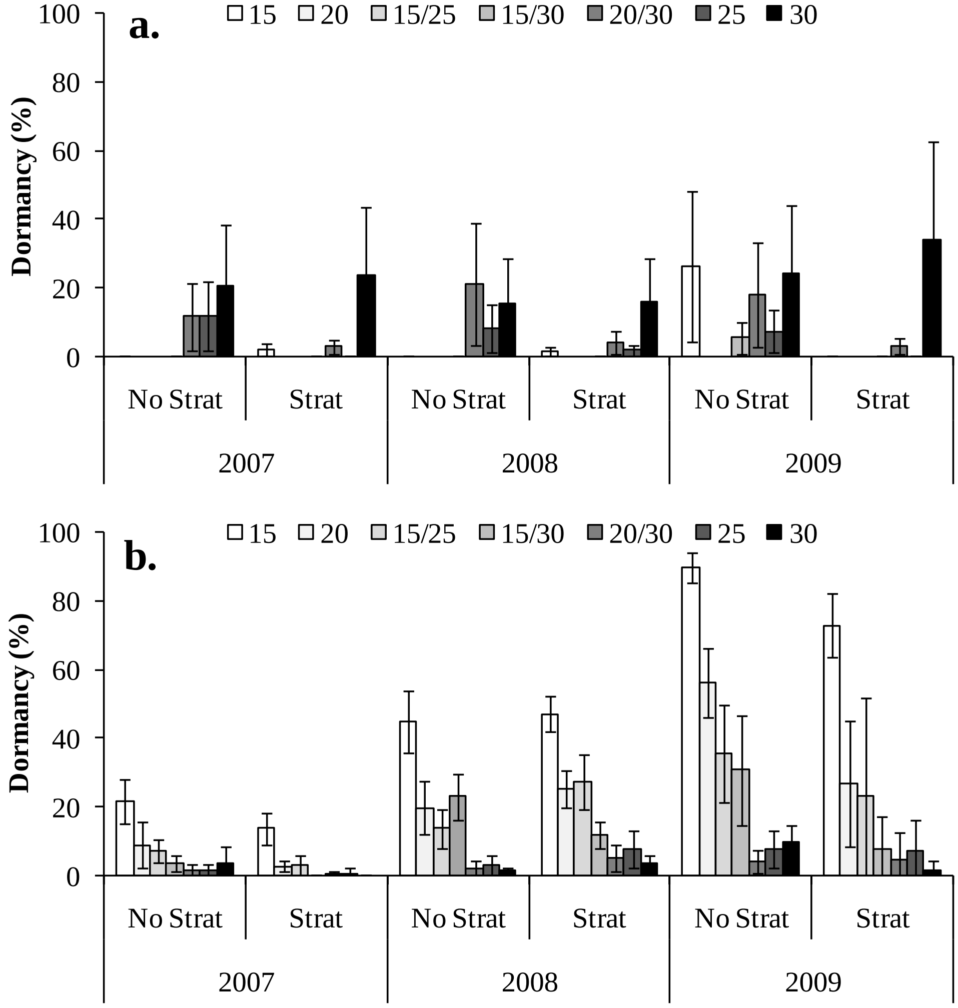

Figure 3. Mean percent dormancy (± 95% confidence limits) of hairy goldaster seeds (*Heterotheca villosa*; a) and prairie dropseed seeds (*Sporobolus heterolepis*; b) by year in response to temperature and stratification temperatures. Values were calculated based on the number of ungerminated seeds that tested positive (tetralozium test) relative to the total number of ungerminated seeds.

MANAGEMENT IMPLICATIONS

Results from our study indicate that hairy goldaster seeds readily germinate under a variety of temperatures less than 30° C. When the species is used for restoration, the most suitable establishment method may be to cast seed in early spring. We found that prairie dropseed has more than one optimal germination temperature, and that responses to both temperature and stratification are strongly influenced by seed collection year. Collection year variability emphasizes the need to evaluate germinability of different seed lots. The best approach for restoration may be to transplant mature individuals into established vegetation (Howell and Kline 1992, Fedewa and Stewart 2009).

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