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Seed Source May Determine Field-Specific Germination and Emergence: The Source by Planting Environment Interaction

Erin K. Espeland,[★] Lora B. Perkins, Matthew E. Horning, and Richard C. Johnson

ABSTRACT

Farm environmental conditions and management practices can result in within-cultivar differences in seed quality and lead to transgenerational plasticity (farm-specific effects on offspring, or TGP) that affect germination and emergence in transplant fields. We used three perennial bunchgrasses, [green needlegrass (*Nassella viridula*) 'Lodorm', slender wheatgrass (*Elymus trachycaulus*) 'Pryor', and bluebunch wheatgrass (*Pseudoregneria spicata*) prevariety registered germplasm P-7] to determine if seeds exhibited TGP. We also determined if TGP was affected by the interaction between production farms and planting environments (farm × environment interaction, or context-dependent TGP), using four laboratory temperature regimes to test germination response and four field environments to test emergence response in 2013. We stored seeds in four different environments for 10 mo before repeating the experiment to test if recent seed storage conditions mitigated TGP. Context-dependent TGP affected emergence for Pryor and Lodorm both years, however, only Pryor exhibited context-dependent TGP for germination in 2013. Sources with low germination and emergence in the field were less likely to exhibit context-dependent TGP. Some transplant fields did not show differences among sources, but in other transplant fields, emergence increased as much as 24% depending on farm source. The effect of recent seed storage conditions, significant only for Pryor, was opposite for germination and emergence, with room-temperature stored seeds exhibiting the highest emergence and lowest germination. Context-dependent TGP in emergence could not be predicted by our coarse information regarding seed production environments and storage conditions or by germination in the lab. Nonetheless, context-dependent TGP significantly determined emergence in two of the three study species. Mechanisms underlying this phenomenon need further study to understand potential benefits and pitfalls for producers and seed buyers.

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Abbreviations: TGP, transgenerational plasticity.

WITHIN CULTIVARS, variation in seed yield and quality among farms is the result of both seed production practices and environmental factors (Elgersma et al., 1994; Liebman, 2000). Seed quality depends on germinable seed and individual seed weight and on field performance, with emergence percentages critical to success in the planting environment. Performance-related seed quality is an expression of maternal effects. For example, larger, well-provisioned seeds often have faster emergence rates (Kalisz, 1986; Stratton, 1989; Van Zandt and Mopper, 2004; but see Galloway, 2001a,b). The expression of maternal effects may differ among planting environments (Miao et al., 1991; Van Zandt and Mopper, 2004) and therefore may be context dependent. A subset of context-dependent maternal effects is adaptive maternal effects; that is, potentially greater germination, emergence, growth, or stress tolerance when the seed-planting environment matches the maternal environment (Dyer et al., 2010; Riginos et al., 2007; Sultan et al., 2009; Violle et al., 2009). Weedy forb species are frequently the subject of maternal effects research (e.g., Alexander and Wulff, 1985; Agrawal, 2002; Biere, 1991; Dyer et al., 2010; Galloway and Etterson, 2007; Platenkamp and Shaw, 1993; Riginos et al., 2007; Sultan et al., 2009), yet there are few studies of maternal effects in long-lived perennial grasses such

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as those used for restoration in the western United States (but see Elgersma et al., 1994; Espeland and Hammond, 2013). Given that both the maternal and paternal environments can affect the phenotypes of offspring (Etterson and Galloway, 2002), the effects of seed production farms on offspring phenotypes are more appropriately termed “transgenerational plasticity” (or TGP, as in Dyer et al., 2010). We currently do not understand if and to what extent TGP associated with seed production environments and postharvest storage (or sources) can promote successful restoration in some locations but not others.

Together with seedling establishment, TGP may affect the adaptive capacity of planted populations. Expression of phenotypic variation can have strong effects on adaptive evolution (Ghalambor et al., 2007; Schlichting and Smith, 2002; Schlichting, 2008), and more variation in response to the environment, either within- or transgenerational, may be linked to greater evolutionary potential (Espeland and Rice, 2012). Although mechanisms for the transmission of maternal effects are not well studied or understood, seed coats clearly influence progeny phenotypes (Lacey et al., 1997). Endophyte infection is a maternal effect (Clay, 1987), and epigenetic alterations resulting from the maternal environment have been found in several plant species (Feil and Fraga, 2012).

In 1999, the native seed industry of the Intermountain and Pacific Northwest region of the United States had a market worth \$3.2 million, and market estimates of the potential for the industry were \$12.2 million (McArthur and Young, 1999). Although current estimates are not available, recent increases in demand for native seeds (Johnson et al., 2010) suggests that the potential value of the industry has substantially increased. The Bureau of Land Management, one of the largest public land managers in the western United States, buys over five million pounds of seed for restoration each year (Havens et al., 2014). These restorations exhibit variable success (James et al., 2011; Peppin et al., 2014) when measured in terms of plant establishment. In addition to plant establishment, soil stabilization, fire control, higher water quality and other ecosystem services (Suding, 2011) are also desirable long-term outcomes of successful restoration.

Seeds are often purchased by federal land agencies and warehoused for future use to ensure that seeds are available in severe wildfire years when demand is high (McArthur and Young, 1999). Generally, seed longevity is promoted by cold, low humidity conditions (Hull, 1973; Mao et al., 2009; Rozman et al., 2010), but not all cultivars within species respond similarly to storage environments as measured by post-storage germination rates (Rozman et al., 2010). Ambient temperature warehousing is a low-cost option for storing native seed, but suboptimal storage conditions might eliminate the benefit of operational decisions to purchase expensive or difficult to

find, locally collected plant materials needed to maximize the potential for successful restoration (Hull, 1973). Little published information regarding the effects of storage on forage grasses such as those used for restoration (Marshall and Lewis, 2004) exists to guide decisions regarding pairing source material with storage environments.

Often, successful landscape restoration in the western United States is constrained by low seedling establishment (James et al., 2011; Peppin et al., 2014). This is likely due to poor germination and emergence associated with conditions such as drought, high competitive pressure from invasive species, and inhospitable seed-bed environments (James and Svejcar, 2010). Therefore, technologies to increase establishment have become a high research priority (Hardegree et al., 2011; James and Svejcar, 2010; Madsen et al., 2012; Rowe and Leger, 2012). We currently have little scientific information to inform decisions regarding where to buy seeds and how to store them, decisions that may result in increased or decreased seed performance in the field. In this study, we manipulated seeds of three native forage grass taxa (two cultivars and one prevariety germplasm, each from a different species) commonly used for restoration to ask if context-dependent TGP was important for establishment at multiple sites in the north-central and northwestern United States. We hypothesized that seed source and recent storage methods would confer context-dependent performance; that is, seeds of the same genetic source produced in different environments or stored under different conditions would germinate and emerge differently in different planting environments, in other words, a seed source \times planting environment interaction would be present.

MATERIALS AND METHODS

Study Species

Bluebunch wheatgrass [*Pseudoregneria spicata* (Pursh) A. Löve] is an outcrossing cool-season bunchgrass native to semiarid regions of the western United States (Larson et al., 2000) and commonly used in restoration (Tilley and St. John, 2013). In 2012, we obtained seeds of P-7 Bluebunch wheatgrass (Jones et al., 2002) from its developer (Tom Jones, USDA-ARS). P-7 is a high-diversity prevariety germplasm created via open pollination of 25 native populations. The seed sources were grown at an irrigated site in Washington state and an unirrigated site near Logan, UT (Table 1).

Green needlegrass [*Nassella viridula* (Trin.) Barkworth] is a cool-season bunchgrass that grows in a variety of soil types in northern Great Plains rangelands in locally sparse populations (Knudson, 2005). This self-pollinating species is often used for restoration in semiarid environments as a minor (<30%) part of planting mixes (Knudson 2005). The cultivar ‘Lodorm’ (Larson and Carter, 1970) was developed from native populations near Bismarck, ND, and was selected for low seed dormancy (Knudson, 2005). We purchased Lodorm seed from the three commercial suppliers that had information regarding the production environment and harvest year (Table 1).

Table 1. Seed sources used for the experiment. Farm locations, harvest years, seed purity percentage, germination (Germ) percentage, and date of tetrazolium (TZ) tests given by suppliers.

Taxon	Farm location	Harvest year	Purity	Germ	TZ date
			———— % ————		
P-7	Logan, UT	2012	–	–	–
P-7	Franklin Co., WA	2012	–	–	–
Lodorm	Montana (MT)	2011	99.95	35	Jul-12
Lodorm	Minnesota (MN)	2012	98.7	95	Aug-12
Lodorm	Franklin Co., WA	2007	97.4	83	Oct-12
Pryor	Franklin Co., WA	2006	96.76	88	Mar-12
Pryor	Bridger, MT	2011	99.59	96	Mar-12
Pryor	Saskatchewan (SK)	2010/2011	99.96	94	Jun-12

Slender wheatgrass [*Elymus trachycaulus* (Link) Gould ex Shinners] is a cool-season bunchgrass native to the northern United States (Ogle, 2002). This self-pollinating species is often used for erosion control because of its good establishment and rapid growth (Ogle, 2002). The cultivar ‘Pryor’ was developed by the Bridger Plant Materials Center especially for use in restoration (Ogle et al., 2012). We obtained seeds grown in Montana from the developer (Joe Scianna, USDA–NRCS) and purchased seeds from the two commercial suppliers that had information regarding production environment and harvest year (Table 1).

Table 1 shows that seed sources for Lodorm and Pryor have different supplier-reported germination fractions and that seeds were harvested in different years. We expect the environment of production, harvesting techniques, and postharvest storage were different among sources.

Laboratory Germination 2013

To test for main effects of seed farm (or source) and planting environment and their interaction under controlled conditions, we germinated seeds in dark growth chambers. A replicate consisted of 20 weighed seeds placed on wet Whatman filter paper in a 4.7-cm diameter petri plate. For each species and source combination, five replicates were placed in four different Percival AR22LC8 (Percival Scientific) growth chambers, programmed at different climates and day lengths in a completely random design. Table 2 shows the different growth chamber programs and indicates that chambers coarsely represent field germination conditions for source locations and planting sites. P-7 was not placed in the Northern chamber (Table 2) because of limited seed numbers. We began the experiment on 31 May 2013 and checked for germination on Day 3, 4, 5, 6, and 21, removing germinates on each date. We defined germination as the point when a radicle visibly emerged from the seed coat.

Field Emergence 2013

To test for main effects of source and planting environment and their interaction under field conditions, we planted seeds for each taxon from all sources (Table 1) in the fall of 2012. We pushed 4-cm lengths of clear plastic tubing (2 cm in diameter) into the soil, leaving less than 1 cm exposed above ground level (hereafter “arenas”). Ten weighed seeds were placed within the resulting arena with seeds buried under less than 3 mm of planting location soil. We planted 10 replicates per species and source

Table 2. Each growth chamber environment described by the high and low temperatures, the number of hours each growth chamber was at the high temperature (cycle), and where each growth chamber may “mirror” average high and low daily temperatures and average day lengths found in likely farm climates in spring and fall within identified production farm locations.

Name	High	Low	Cycle	Mirror
	———— °C ————		h	
Northern	18	3	15.5	SK (May)
Mild	21	7	15	SD, WA (May)
Mountain	20	4	14.75	UT, MT, MN (May), WA (Apr)
Cold	14	1	13.5	SD, MN, UT (Apr), MT (Oct)

Table 3. Climate characteristics of planting locations: mean annual temperature (MAT), mean annual precipitation (MAP), mean winter temperature (MWT), mean summer temperature (MST), mean winter precipitation (MWP), and mean summer precipitation (MSP) based on 1981 to 2009 normals.

Location	MAT [†]	MAP [†]	MWT [†]	MST [†]	MWP [†]	MSP [†]
MT1	5.9	350	–8.3	19.6	31	153
WA1	11.5	336	–1.9	12.5	116	44
OR	8.1	285	0.6	16.5	116	46
SD	6.2	617	–0.8	13.2	154	480
MT2	7.4	387	–4.5	19.8	47	128
WA2	8.7	587	–0.1	17.9	197	84

[†] Temperatures are reported in °C, precipitation values are reported in mm; http://climate.sdstate.edu/climate_site/climate_page.htm (accessed 13 May 2015); <https://www.ncdc.noaa.gov/oa/climate/normal/usnormals.html> (accessed 15 Jan. 2015).

combination in a completely randomized manner at four field locations. Planting locations were in a conservation reserve program field (cultivated pastureland) near Bloomfield, MT (MT1), at the Central Ferry experimental farm (cropland) in southeastern Washington (WA1), at the USFS Deschutes National Forest Supervisor’s Office (temporary grassland) in Bend, OR (OR), and at the Natural Resource Management “Research Farm” (cultivated pastureland) at South Dakota State University in Brookings, SD (SD). Table 3 shows historical climate data for these locations. Plantings were established at WA1 on 29 October, SD on 23 October, MT1 on 18 October, and OR on 8 November. We counted emergent seedlings (coleoptile extended above the soil surface) in April (OR, WA1), May (MT1), and June (all sites). Maximum observed number of plants per arena was used as the dependent variable for statistical analysis.

Recent Storage Conditions

To test the effect of seed storage on germination and field emergence, we placed seeds from each species and source combination under four different conditions for over 10 mo. Seeds (except both sources of P-7 and Pryor grown in Montana because of limited seeds) were placed in: a refrigerator (4 °C), at room temperature (20–21 °C), and two unheated storage facilities (Stacey and Miles City, MT) on 26 Apr. 2013. Hobo U10-001 dataloggers (Onset Computer Corporation) were placed with the seeds to track temperature in the ambient environments (Fig. 1). We removed seeds from storage on 3 Mar. 2014 and kept them at room temperature before subsequent experiments.

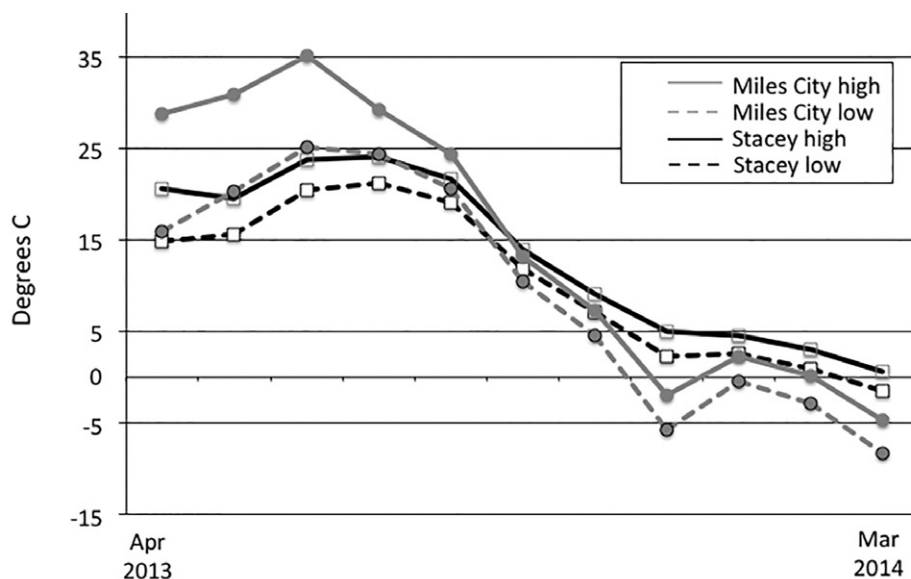


Figure 1. Monthly average seed storage temperatures in Stacey, MT, and Miles City, MT.

Laboratory Germination 2014

The 2014 laboratory germination trial tested main effects of source, storage conditions, chamber environment and their interactions under controlled conditions. The trial was run June 9 through July 28 (starting on June 9 for the Mountain and Northern treatments and July 11 for the Cold and Mild treatments). Similar to the 2013 experiments, we placed five replicates of 10 weighed seeds per petri dish per source and storage combination in four chambers programmed as in 2013 (Table 2). Northern and Mild chambers were Percival models AR22LC8, Mountain was Percival model E36HO, and we used Percival model 130NLC8 for the Cold environment because of limited availability of AR22LC8 chambers for this experiment. We checked for germination at Days 3, 7, and 21, and removed germinates on each date.

Field Emergence 2014

The 2014 field emergence trial tested main effects of source, storage conditions, field planting location, and their interactions under field conditions. Locations and planting protocols for 2014 were the same as 2013, with three replicates per species, source, and storage combination (described in the above paragraphs). We planted an additional site in eastern Washington at the NRCS Plant Material Center (cropland) in Pullman, WA (WA2), and an additional site in a hayfield (cultivated pastureland) near Ashland, MT (MT2). Planting dates were: WA2, 21 April; WA1, 28 April; MT2, 30 April; MT1, 5 May; SD, 7 May; and OR, 13 May. We checked plots weekly for 6 wk and then every other week for an additional 4 wk. Maximum observed number of plants per arena was used as the dependent variable for statistical analysis.

Data Analysis

All analyses of variance were completed using the mixed procedure (Proc Mixed) in SAS/STAT version 9.2 as described in Littell et al. (1996). Separate analyses were completed for each species for all experiments with seed weight included as a covariate.

For laboratory germination tests in 2013, the effects of source, chamber environment, and the source by chamber interaction were determined on seeds. The seed sources were nested within four chambers, each representing one of the four environments (Table 2). Chamber environment and source were fixed and the replicates within chambers were random. In 2013, plant emergence in field locations was analyzed, with seed source nested within planting location. Chamber environment, source, and location by source were fixed effects, and replicates within chamber, random.

For laboratory germination tests in 2014, both source and storage environment were nested within the four chamber environments. Those factors and associated interactions were fixed effects and replicates within chamber were random.

When significant effects were found, we ran Tukey's Highly Significant Difference tests ($P < 0.05$) to determine differences among levels of experimental factors. Significant main effects are not discussed in detail when interactions were significant. When seed weight was significant but the regressions had R^2 of less than 0.05, the regressions are not reported. Numbers of seeds or plants were the dependent variables in the analyses, but percentages (\pm one standard deviation) are reported in the results section.

RESULTS

Source and Environment, Lab Germination

Slender wheatgrass Pryor was the only taxon that exhibited a significant source by environment interaction in laboratory germination and only in 2013 (Table 4). P-7 had remarkably stable germination across all chamber environments in 2013 (Fig. 2a). In 2013, Pryor grown in MT had similar germination in all chamber environments (Fig. 2b). There were large differences between SK-source and WA-source seed with WA germination lowest in the Northern and Cold environments, and germination of the SK source was relatively high in all but the Cold environment (Fig. 2b). The interaction between source and chamber environment was not significant for Lodorm in either year. (Table 4, Fig. 2c).

Table 4. Analyses of variance summary of laboratory germination tests for bluebunch wheatgrass (prevariety P-7), green needlegrass (cultivar Lodorm), and slender wheatgrass (cultivar Pryor) on seeds from different farm sources and in different growth chamber environments in 2013. Numerator (Num) degrees of freedom, denominator (Den) degrees of freedom, *F* value, and *P* are shown for each factor. For 2014 the effect of different recent seed storage conditions was also evaluated.

Effect	Num DF	Den DF	<i>F</i> value	<i>P</i>
P-7 2013†				
Source	1	51	2.71	0.1060
Chamber‡	2	51	0.72	0.4910
Source × chamber	2	51	2.93	0.0623
Seed weight	1	51	2.00	0.1640
Lodorm 2013				
Source	2	107	113.06	0.0001
Chamber	3	107	2.31	0.0806
Source × chamber	6	107	0.80	0.5720
Seed weight	1	107	4.87	0.0295
Pryor 2013				
Source	2	99.6	373.50	<0.0001
Chamber	3	16.1	13.46	0.0001
Source × chamber	6	91.4	9.95	<0.0001
Seed weight	1	106	0.13	0.7205
Lodorm 2014				
Source	2	395	73.73	<0.0001
Chamber	3	36	2.05	0.1246
Storage§	3	395	0.30	0.8249
Source × storage	6	395	1.65	0.1312
Source × chamber	6	395	1.46	0.1919
Storage × chamber	9	395	0.76	0.6508
Source × storage × chamber	18	395	0.90	0.5760
Seed weight	1	395	4.26	0.0398
Pryor 2014				
Source	1	251	703.90	<0.0001
Chamber	3	36	39.30	<0.0001
Storage	3	251	5.82	0.007
Source × storage	3	251	4.05	0.0078
Source × chamber	3	251	1.20	0.3110
Storage × chamber	9	251	2.08	0.0321
Source × storage × chamber	9	251	2.00	0.0403
Seed weight	1	251	0.31	0.5771

† P-7 was not included for 2014 because of limited seed.

‡ See Tables 1 and 2 for farm sources and growth chamber environments.

§ Seed storage conditions were for 10 mo at 4°C, 20 to 21°C, and ambient conditions at Stacey and Miles City, MT (Fig. 1).

On the basis of the different germination percentages initially reported for purchased seed (Table 1), we expected a main effect of source on germination. Both Lodorm and Pryor exhibited a main effect of farm source on total seed germination in 2013 (Table 4). Pryor grown in MT had 96% (± 6) germination, SK-grown seed had 81% (± 16), and WA-grown seed, 26% (± 20) germination. Lodorm grown in MN had 66% (± 15) germination; MT-grown seed, 58% (± 16); and WA, 29% (± 15) germination. Source remained significant in 2014 for both species. Pryor grown in SK

exhibited 78% (± 16) germination and WA-grown seed, 19% (± 16). Lodorm grown in MN had 55% (± 22) germination; MT, 57% (± 17); and WA, 32% (± 19).

Temperature-determined germination is common; therefore, we expected a main effect for chamber temperature environment on germination percentages. Chamber was significant only for Pryor in both years (Table 4). In 2013, Mountain chamber conditions resulted in 79% (± 28) germination; Mild, 74% (± 25); Northern, 62% (± 43); and Cold, 56% (± 35). In 2014, Pryor grown in Mountain conditions had 50% (± 30) germination; Mild, 55% (± 35); Northern, 56% (± 33); and Cold, 34% (± 32).

Seed Weight, Lab Germination

Seed weight (total weight of the seeds per dish) was a significant predictor of germination in the laboratory only for Lodorm (Table 4), and this was true in both years. Explanation of variation was very low, with R^2 values equal to 0.04. There was a positive relationship between seed weight and germination.

Recent Storage, Lab Germination

Recent storage environment was a significant main effect for Pryor in 2014, and storage interacted with chamber environment and source in a three-way interaction (Table 4). The three-way interaction did not result in any change in rank among source populations: SK-grown seeds always tended toward higher germination (58 to 92%) than WA-grown seeds (2 to 44%). However, this difference was not always significant, as indicated by the three-way interaction (Table 4).

Source and Location, Field Emergence

P-7 exhibited a response to planting location (Fig. 3a), but there was no interaction between source and location (Table 5). Similar to results for other taxa, P-7 tended toward highest emergence in SD, with MT1 and OR intermediate and lowest emergence at WA1. Both Lodorm and Pryor exhibited a significant response to the interaction between source and field location in both 2013 and 2014. All sources of Pryor performed best in the SD planting environment in 2013, MT-grown seeds performed equally well at MT1 and OR, and SK-grown seeds performed better in MT1 than OR (Fig. 3b), and a similar pattern occurred in 2014 (Fig. 3c). In 2013, Lodorm had the highest emergence rates in SD and lowest in OR (Fig. 3d). WA-grown emergence was not statistically distinguishable among planting locations, whereas MN-grown seeds performed very poorly at both OR and WA1 planting locations, with zero emergence in OR (Fig. 3d). These results were repeated in 2014, with WA-grown seeds emerging reliably (but poorly) across locations (Fig. 3e). Lodorm grown in MN had high emergence at WA2, significantly better than at MT1. Lodorm grown in MT also had significantly lower emergence at MT1 than SD (Fig. 3e).

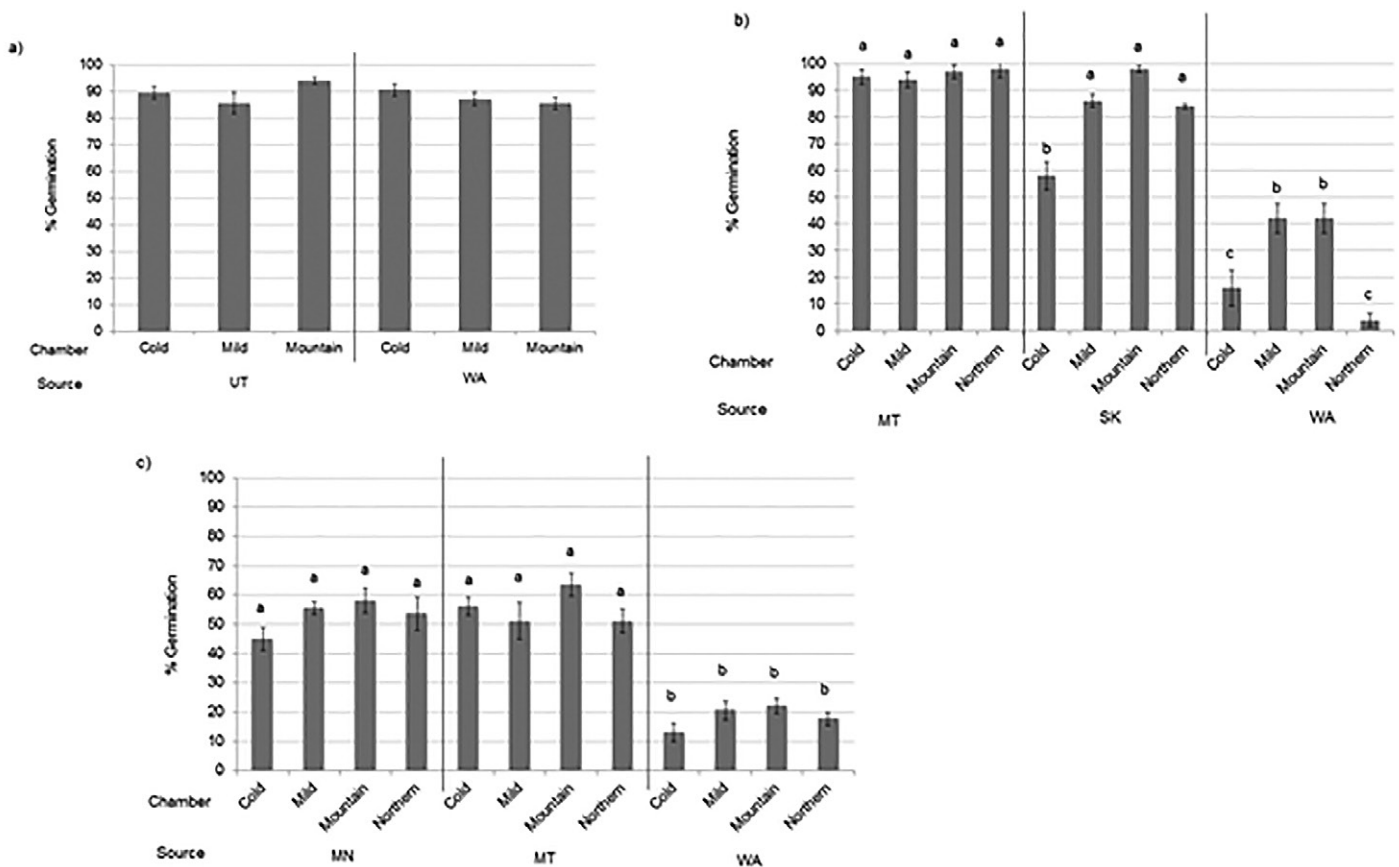


Figure 2. Germination percentage by chamber environment (Table 2) and source: (a) bluebunch wheatgrass prevariety P-7, (b) slender wheatgrass cultivar Pryor, and (c) green needlegrass cultivar Lodorm, 2013. Bars indicate one standard error. Different letters within panels indicate significant differences.

Source was a significant main effect in all the field trials of Lodorm and Pryor, but not for P-7 (Table 5). For both Lodorm and Pryor, WA-grown seed performed poorly compared with the other sources. Planting location was a significant main effect on emergence in every trial except Lodorm in 2014 (Table 5, Fig. 3e).

Seed Weight, Field Emergence

Seed weight (weight of the 10 seeds planted in grams) significantly affected only Pryor emergence in 2013 (Table 5): Percent germination = $10 \times (-2.0 + 100.1 \times \text{seed weight})$, $R^2 = 0.08$, $p = 0.0014$.

Recent Storage, Field Emergence

Storage was a significant main effect only for Pryor in the field (Table 5): Stacey-stored seed emergence of 8% (± 18); Refrigerator, 11% (± 23); Miles City, 14% (± 22); and Room Temperature, 20% (± 26) emergence.

DISCUSSION

Seed producers expect that their seeds will have different emergence percentages in different environments: clearly, stressful environments will reduce the number of plants that emerge. However, some sources were better able to emerge in stressful environments: for example, MT-grown

Pryor had high emergence in OR in 2013. The large differences in emergence within sources among planting environments (Fig. 3) demonstrate potential tradeoffs between reliability and mean performance. In 2013, emergence of Pryor grown in WA was reliable (the same across sites), but lower than SK- and MT-grown seeds when all sources were planted in SD. Similarly, WA-grown Lodorm seeds also performed reliably in 2013 and 2014. However, MN-grown Lodorm performed very well (with sometimes double the emergence of WA-grown seeds) at SD and MT1 in 2013, and in 2014 MN-grown Lodorm had more than 10 times the emergence of WA-grown seeds at WA2.

We found that recent storage conditions affected Pryor emergence and lab germination in opposite ways: Room Temperature stored seed germinated poorly in the lab, but emerged the best in the field. Results of other research using forbs on the interactions of storage environment with maternal environment are mixed, with studies finding no interaction (Biere, 1991; Platenkamp and Shaw, 1993) and others with interactive effects (Alexander and Wulff, 1985; Schmitt et al., 1992). Research on seed storage effects for forage grasses has shown that variation in germination can interact with storage methods, and that even the way the seeds are packaged can alter germination rates in some storage environments (Marshall and Lewis,

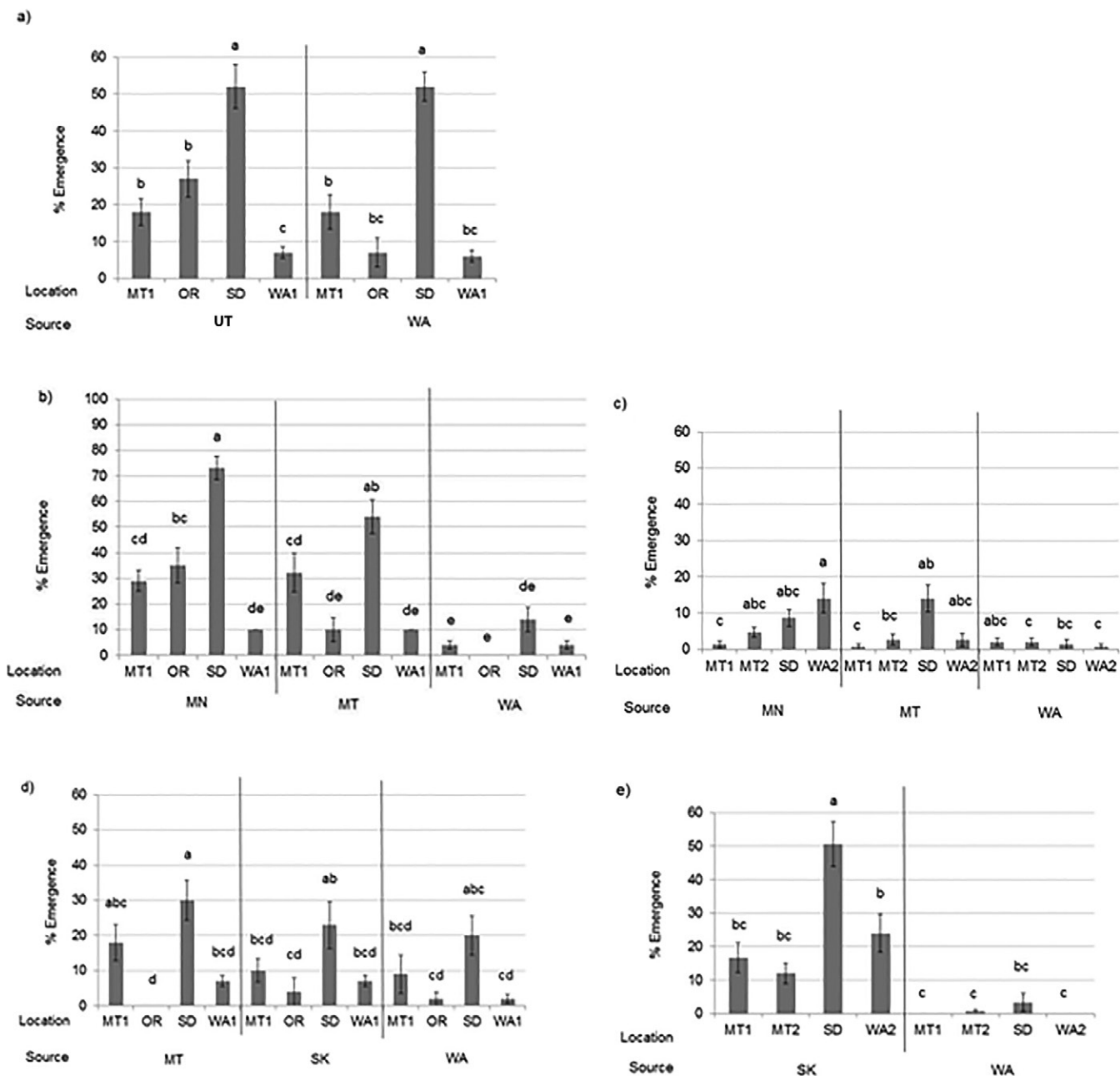


Figure 3. Effects of sources (Minnesota [MN], Montana [MT], Saskatchewan [SK], Utah [UT], and Washington [WA]) and planting locations (Montana [MT1 and MT2], Oregon [OR], South Dakota [SD], and Washington [WA1 and WA2]) on field emergence of slender wheatgrass cultivar Pryor and green needlegrass cultivar Lodorm in 2 yr and on bluebunch wheatgrass prevariety P-7 in 1 yr: (a) P-7 2013, (b) Pryor 2013, (c) Pryor 2014, (d) Lodorm 2013, (e) Lodorm 2014. Bars are one standard error. Different letters within panels indicate significant differences.

2004). Longer storage times before the experiment for the two cultivars from WA sources (Table 1) may have led to their poor germination and emergence overall.

Field emergence rates of Lodorm were dramatically reduced in 2014, with emergence percentages about one-half of 2013, but there appeared to be no such difference for Pryor. Laboratory tests showed that both cultivars had similar germination rates in controlled conditions across years. In the northern Great Plains, sowing green needlegrass in spring is not recommended (Wayne Duckwitz, USDA–NRCS, personal communication, 14 Nov. 2014),

and the poor field performance of Lodorm in 2014 may be because seeding was performed in spring of that year.

We conducted laboratory investigations to find a bioassay to predict seed source by planting field interactions. Our results show that laboratory investigations based on varying germination temperatures may not predict variability in emergence in situ. Pryor germination and emergence were both context-dependent TGP in each year. However, Lodorm exhibited context-dependent TGP in the field but not in the lab, and this was the case in both years. This calls into question whether laboratory studies

Table 5. Summary of analyses of variance of field emergence tests for bluebunch wheatgrass (prevariety P-7), green needlegrass (cultivar Lodorm), and slender wheatgrass (cultivar Pryor) on seeds from different farm sources and in different locations in 2013. Numerator (Num) degrees of freedom, denominator (Den) degrees of freedom, *F* value, and *P* are shown for each factor. For 2014 the effect of different seed storage conditions was also evaluated.

Effect	Num DF	Den DF	<i>F</i> value	<i>P</i>
P-7 2013[†]				
Source	1	35.1	2.33	0.1356
Location	3	35.6	7.52	0.0005
Source × location	3	35.1	0.29	0.8327
Seed weight	1	69.1	0.27	0.6082
Lodorm 2013				
Source	2	81.5	28.29	<0.0001
Location	3	38.8	40.22	<0.0001
Source × location	6	72	14.04	<0.0001
Seed weight	1	104	2.85	0.0943
Pryor 2013				
Source	2	107	16.01	<0.0001
Location	3	107	90.58	<0.0001
Source × location	6	107	8.76	<0.0001
Seed weight	1	107	4.52	0.0357
Lodorm 2014				
Source	2	29.4	6.86	0.0017
Storage [‡]	3	87.2	1.17	0.3250
Location	3	7.91	2.45	0.1390
Source × storage	6	87.2	0.23	0.9665
Source × location	6	87	2.95	0.0115
Storage × location	9	87	0.65	0.7549
Source × storage × location	18	87	0.81	0.6787
Seed weight	1	93.8	2.01	0.1591
Pryor 2014				
Source	1	63	19.66	<0.0001
Storage	3	63	2.92	0.0407
Location	3	63	14.20	<0.0001
Source × storage	3	63	1.42	0.2440
Source × location	3	63	9.91	<0.0001
Storage × location	9	63	0.22	0.9904
Source × storage × location	9	63	0.35	0.9533
Seed weight	1	63	0.06	0.8083

[†] P-7 was not included for 2014 because of limited seed.

[‡] Seed storage conditions were for 10 mo at 4°C, 20 to 21°C, and ambient conditions at Stacey and Miles City, MT.

on TGP such as Espeland and Hammond (2013) accurately reflect the potential for expression in the field.

There were many factors combined within each source: growing conditions, harvesting techniques, number of on-farm generations from foundation seed, and postharvest storage conditions likely vary among farms as well as among harvest years. For P-7, some of this variation was controlled: seeds had been harvested in the prior year, and we know that production fields were planted with seed direct from the breeder. The lack of variation between factors that contribute to “source” may explain

the lack of TGP for this taxon. The variance in factors contributing to source in our experiment did not lead to different emergence among sources at SD, MT2, or WA1 planting locations. This indicates that some planting sites may not be vulnerable to the effects of TGP on plant establishment. Our experiments provide no straightforward evidence for coarse-scale adaptive maternal effects (as in Dyer et al., 2010): WA-grown seeds never performed best at WA planting locations. This leaves practitioners with a dilemma as to how to ensure the maximum possible seedling establishment per dollar spent on seeds. With limited information so far as to the mechanism for the link between source and variance in establishment, the choice of how to proceed may be aesthetic. Some practitioners may choose to bet-hedge and use seeds from multiple sources for each planting. Some may choose to retain a source that they have already identified as providing adequate performance. And some may choose to evaluate success of multiple sources over the course of several years and choose the source with either (i) the most reliable performance or (ii) the highest mean performance, depending on his or her risk aversion level.

That said, there are a few cautions against direct application of our results to restorations. Sometimes seeds are actively managed from the acquisition of certified seed through production (seed increase) and eventual destination seeding, and more is known regarding the provenance of seeds throughout the materials management process. It was difficult for us to gain information from seed suppliers regarding the exact locations of seed production farms, therefore the cultural and environmental factors that could have conferred TGP in these farms are unknown. Seed storage durations before our purchase varied (Table 1), and storage conditions are unknown. In addition, only a single harvest year was tested for each source, and outcomes may change among harvest years. We did not transplant seed into real restoration environments: in particular the seed bed environment at experimental farms such as WA1, WA2, and SD may have provided a poor proxy for restoration seed beds, where seed bed preparation and soil conditions are often not optimal (Espeland and Perkins, 2013; Espeland, 2014). We do not know if subsequent harvest years from the same farms would yield similar results; we expect year to year variation in TGP because it is a response to environmental factors that include rainfall amount and pattern. In addition, the number of reseeded generations in the production fields is also unknown, and on-farm selection may have taken place (as in Goldringer et al., 2006). While these limitations constrain our ability to determine the biological basis for the emergence differences we observed in this experiment, the experimental setup accurately reflects contributing factors to seed performance in the most commonly encountered, real-world setting.

Most of the detailed demographic work on establishment of perennial grasses in the United States has been performed in the Great Basin and Intermountain West. Other researchers have observed native grass establishment rates of 17 to 75% (Uselman et al., 2014) in small experimental plots, and high germination (as much as 79%) followed by low emergence (4 to 17%) in post-fire plots (James et al., 2011; James and Svejcar, 2010). Fire may lead to seed bed environments that are particularly inhospitable, with low establishment rates—another study found establishment rates to be as low as 0.75% in post-fire soils (Madsen et al., 2012). The clear plastic arenas used to track emergence helped protect seeds from ant predation and may have contributed to emergence rates that were sometimes relatively high. We observed wide variation in performance among the Intermountain West locations (OR, WA1, WA2), where two locations had zero emergence in 2014, and the highest emergence that year was at WA2 with Lodorm at 14% and Pryor at 23%. Variability among northern Great Plains locations (MT1, MT2, SD) was less dramatic because there were no locationwide seeding failures. South Dakota generally exhibited the highest emergence rates (over 70% for MN-grown Pryor in 2013) and only sometimes differed from MT locations. The two MT locations did not differ from one another.

As we observed in this study, the effect of source and planting location on seed emergence can be large and interactive. Variation in plant establishment at many restoration locations may be increased or decreased depending on TGP generated within sources. Stressful production environments may reduce the potential for context-dependent TGP (Dyer et al., 2010; Espeland and Rice, 2012), therefore context-dependent TGP may be minimized by some management practices. In forestry contexts, seed production areas (i.e., orchards) are often installed in environments that prompt trees to produce more cones (Faulkner, 1975). Some perennial grass seed farmers regularly burn their fields to control disease and increase yields (Hardison, 1980), and it is unknown if this type of management may also limit context-dependent TGP. Understanding how seed production environment, postharvest storage, and recent seed storage influence the establishment of seeds has the potential to greatly increase the efficacy of restoration plantings and enhance the recovery rate of degraded landscapes.

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