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RESEARCH ARTICLE

Managing contingency in semiarid grassland restoration through repeated planting

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The success of grassland restoration in semiarid regions is contingent on good establishment years. Here it is asked whether success rate can be increased by planting repeatedly among years, or by consistently using high planting densities. I planted seeds of a dominant native perennial grass, *Elymus lanceolatus*, at five densities (range: 30–3000 seeds/m^2) in each of 3 years. *Elymus* seedling emergence and cover increased significantly with planting density. Cover after three growing seasons was maximized (i.e. not significantly different from the greatest cover) at planting densities of 300–600 seeds/m^2. On the other hand, low germination in a dry warm year resulted in density having no effect on cover 3 years later. Two favorable planting years showed trajectories to native dominance after three growing seasons. In contrast, one unfavorable planting year showed a trajectory of non-native dominance. Emergence was increased modestly by both herbivore and interspecific neighbor removal. Overall, the most economical process for ensuring success (assuming that seed costs are high and planting and site-preparation costs are low) may be to plant at moderate density (300–600 seeds/m^2) in repeated years until a favorable year is encountered.

Key words: climate, competition, cover, *Elymus lanceolatus*, emergence, establishment, herbivory, prairie

Implications for Practice

- Repeated planting among years may assure restoration success (high cover of native species) in grasslands characterized by great among-year variation in rainfall.
- Native plant cover can be increased by planting greater seed densities, but only in years with sufficient rainfall.
- In years with good establishment, planting 300–600 seeds/m^2 is likely to produce native grass dominance.

Introduction

Restoring native species to semiarid North American grasslands is challenging, partly due to the great among-year variation in precipitation that characterizes this ecosystem (Knapp et al. 2002). Consequently, restoration success is contingent on weather and varies greatly among years (Bakker et al. 2003). Contingency can be overcome with repeated seeding: failures in years with weather unsuitable for establishment can be compensated for by successes in other years (MacDougall et al. 2008). This strategy, however, is expensive and difficult to plan and budget for, as successes and failures cannot be predicted.

Planting at high density increases restoration success (Simmons 2005; Sheley et al. 2006; Carter & Blair 2012; Carrington 2014), but its utility in addressing contingency (i.e. providing good establishment in dry years) is unknown. There are two mechanisms by which planting at high density could address contingency. First, high planting rates can act as insurance by creating a seed bank of native species that will be present in later years with more favorable conditions (Simberloff 2009). This approach worked in an old field: planted native species failed to germinate in the year of planting but appeared in the second year (Wilson & Gerry 1995). Second, high planting rates of native species generally decrease populations of undesired non-native species (Stevenson et al. 1995; Sheley et al. 1999; Simmons 2005; Carter & Blair 2012), which should result in less competition from those species in the future.

Against these positive effects, high planting density that produces high seedling density during a wet spring could lead to low seedling survival as seedlings compete (Mueggler & Blaisdell 1955; Leyshon et al. 1981; Bakker et al. 2003), especially in the late-summer drought characteristic of the North American Great Plains (James et al. 2003). Further, high planting density cannot overcome dry years if there is little germination in dry years (Carter & Blair 2012), or if survival in the seed bank is low due to granivory (Orrock et al. 2008; Maron et al. 2012). Finally, as in the case of repeated planting, high densities may be wasteful if relatively few seedlings establish: a meta-analysis of 27 seed addition studies found that on average, only 14% of planted seeds germinate (Clark et al. 2007). Clark et al. (2007) propose that establishment limitation exceeds seed limitation, suggesting limited benefits from high planting density.

Author contributions: SW conceived and designed the research, performed the experiments, analyzed the data, and wrote the manuscript.

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In addition to among-year variability in germination driven by weather, two biotic factors frequently limit restoration success, herbivory (Howe et al. 2002; MacDougall & Wilson 2007; Orrock et al. 2008; Maron et al. 2012; Drystek & MacDougall 2014) and interspecific competition from neighboring plants (Bakker & Wilson 2004; Baer et al. 2005; Cox & Allen 2011; Richardson et al. 2012). Few studies have examined how these factors vary among years.

In this study the following questions were raised: (1) Can the contingency of restoration success in semiarid grassland can be overcome by planting repeatedly in successive years, or by using high seeding densities; and (2) are the impacts of herbivory and competition on restoration variable across years?

Methods

An abandoned field in southern Saskatchewan (50°16′N, 104°17′W) that had been cropped for about a century and then tilled annually for about 15 years for weed control was studied. Climate is continental. The mean annual temperature for Regina, 30 km NW of the study site, is 3.0°C (1976–2006, www.weather.gc.ca). The mean annual precipitation is 380.3 mm with most precipitation falling in the summer. The soil is a clay regosol (Soil Research Institute 1964). Grasslands in the area prior to cultivation were mixed-grass prairie dominated by *Elymus lanceolatus* and *Koeleria macrantha* (Shorthouse 2010).

I planted seeds of *E. lanceolatus* in 3 years (2005–2007) and followed the outcome for at least three growing seasons. *Elymus* was planted because it is a tall, rhizomatous species that competes well with non-native species and establishes better than other native grasses (Bakker & Wilson 2004). Although the response of diverse communities is of great interest, only one species was used in this experiment to avoid confounding effects of interspecific interactions.

Seeds are planted at five densities (30, 300, 600, 1800, and 3000/m^2) in early June each year in 2005–2007. The density of seeds under natural prairie falls within the range of 1000–3000 seeds/m^2 (Iverson & Wali 1982; Grilz et al. 1994). Some rates of restoration (30–35 seeds/m^2) (Duebbert et al. 1981; Howe et al. 2002) are low relative to natural density, but high research rates (4000–12,500/m^2) (Sheley et al. 1999; Hutchings & Stewart 2002) may be wasteful.

In addition, there were two additional treatments at 1800 seeds/m^2: no herbivores and no interspecific neighbors. Thus, the total number of treatments was seven, with five replicates of each treatment, for a total of 35 plots (each 1×1 m) each year. Treatments for each year were arrayed in a completely randomized design in a row of adjacent plots. Rows for each year were 2 m apart.

Plots that were planted in any given year were cultivated 10 cm deep using a shovel cultivator and then harrowed in late May, 1–2 days before planting. Each planting year, seeds of *Elymus* were taken from a common pool stored in darkness at 8°C.

Herbivores were excluded by surrounding plots with hardware cloth (50 cm tall, 1-cm mesh), buried 5 cm in the soil, and topped with 15 cm of aluminum flashing designed to discourage climbing by small mammals (mostly voles [*Microtus* sp.] and white-footed deer mice [*Peromyscus* sp.]; S. Wilson, personal observation). Shade from the flashing was not expected to influence germination, given the high altitude of summer sun and the narrow width of the flashing. Exclosure tops were covered with fine plastic netting (2-cm mesh) that excluded birds. No sign of herbivores was found within the exclosures. Exclosures remained in place during the first year of each planting year. Interspecific competitors were removed by hand-weeding every 3 weeks until mid-July and monthly thereafter during the first year of each planting year.

Seedling density of *Elymus* was counted near 1 July and mid-September in the first year of each planting year. Emergence was defined as July seedling density. Establishment was defined as September density expressed as a proportion of July density. The cover of each species was measured using Daubenmire's scale in mid-September of the first and third years after planting. In addition, cover was measured each year for plots planted in 2005, and in 2009 for plots from all planting years.

Two-factor analysis of variance (ANOVA) tested the hypotheses that emergence, establishment, cover of *Elymus*, and the cover of non-native species varied among planting densities and planting years. Density was treated as a nominal variable instead of a continuous one because it had fixed levels. Pairwise contrasts within ANOVA tested for differences among densities. Plots with herbivores excluded and competitors removed were not included in these analyses. Separate two-factor ANOVAs tested whether the dependent variables in plots planted at 1800 seeds/m^2 varied among treatments (control, no herbivores, and no competitors) and planting years.

Results

Weather During the Study

Growing-season (June–August) temperature, relative to the 30-year mean (17.7°C), was slightly below average (17.0) in 2005 but above average in 2006 (18.3) and 2007 (18.2) (Fig. S1, Supporting Information). Growing-season precipitation, relative to the 30-year mean, (178.6 mm), was near average in 2005 (165.9), but below average in 2006 (115.5) and 2007 (117.4).

Density and Planting Year

Emergence in year 1 (i.e. at the end of the first growing season in each year of 3 years of planting) increased significantly with planting density and varied significantly among planting years (Fig. 1A–C; Table 1). Emergence in 2005 and 2006 was about threefold greater than in 2007. There was no significant interaction between planting density and planting year.

Establishment in year 1 (September density expressed as a proportion of July density) did not vary significantly with planting density, but did vary significantly among planting years, and with the interaction between planting

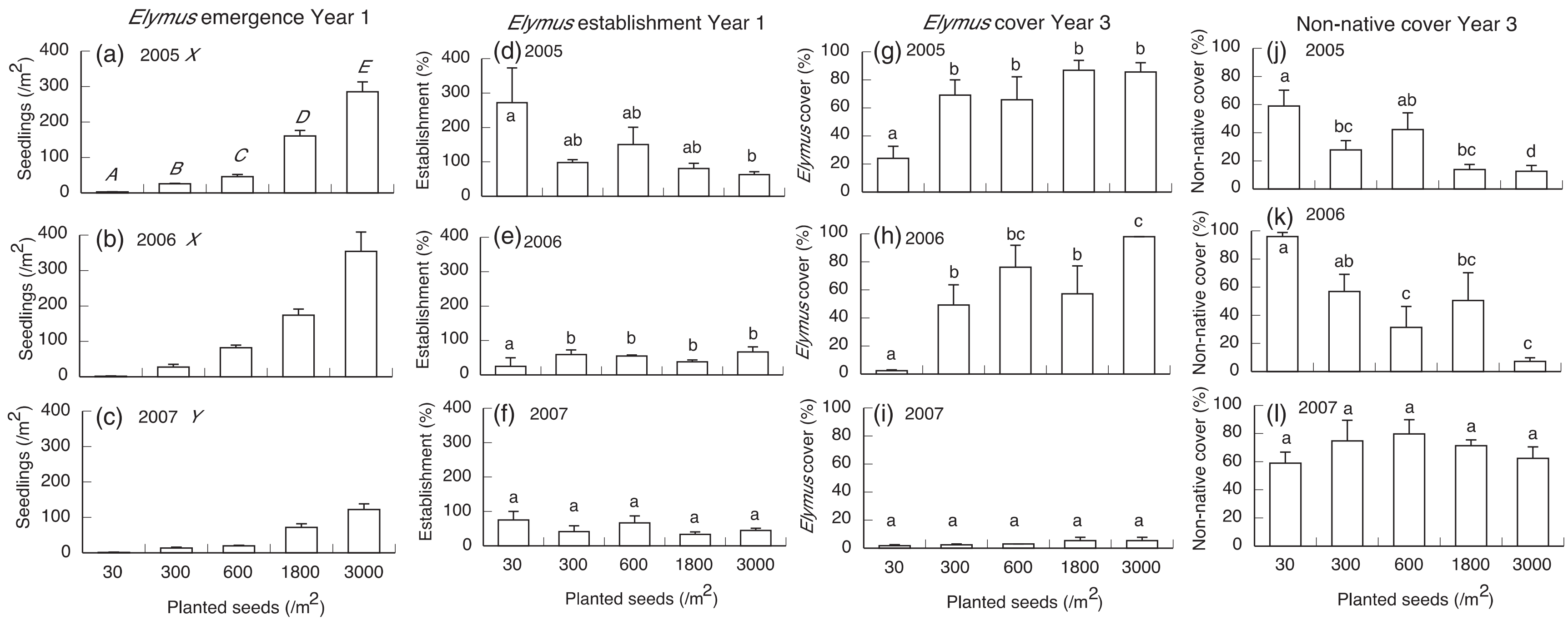

Figure 1. (A–C) Emergence of seedlings (mean + SE) of the native grass *Elymus lanceolatus* in three planting years (2005–2007) as a function of planting density. Emergence varied significantly ($p < 0.05$) with planting density and planting year (Table 1). *A–E*: Means of planting density treatments with different letters are significantly different. *X*, *Y*: Means of planting years with different letters are significantly different. (D–F) Establishment of *Elymus* in three planting years as a function of planting density. Establishment varied significantly with the interaction between planting density and planting year (Table 1). a, b: means of each planting density in each year with different letters are significantly different. (G–I) Cover of *Elymus* 3 year after planting in each of 2005–2007 as a function of planting density. Cover varied significantly with the interaction between planting density and planting year (Table 1). a–c: Means of each planting density in each year with different letters are significantly different. (J–L) Total cover of non-native species 3 years after planting in each of 2005–2007 as a function of planting density of *Elymus*. Cover varied significantly with the interaction between planting density and planting year (Table 1). a–c: Means of each planting density in each year with different letters are significantly different.

Table 1. ANOVA results for effects of planting density and planting year on the emergence, establishment and cover of the native grass *Elymus lanceolatus*, and the cover of non-native species (error df = 90).

Source	df	SS	F	p
Emergence				
Density	4	34.27	300.54	<0.001
Year	2	2.19	38.39	<0.001
D × Y	8	0.31	1.39	0.220
Establishment				
Density	4	0.77	1.38	0.254
Year	2	4.24	15.24	<0.001
D × Y	8	7.10	6.37	<0.001
Native cover				
Density	4	6.84	12.89	<0.001
Year	2	2.03	7.66	0.001
D × Y	8	2.42	2.28	0.033
Non-native cover				
Density	4	3.28	10.81	<0.001
Year	2	2.87	18.95	<0.001
D × Y	8	2.84	4.68	<0.001

df, degrees of freedom.

density and planting year (Table 1). Establishment decreased with planting density in 2005, increased with planting density in 2006, and was unaffected by planting density in 2007 (Fig. 1D–F).

Cover of *Elymus* at the end of the third growing season for each planting year varied significantly with planting density, planting year, and their interaction (Table 1). For plots planted in 2005, cover was significantly lower at the lowest planting density (Fig. 1G). Plots planted in 2006 showed similar results, although with some variation among the higher planting densities (Fig. 1H). In contrast, plots planted in 2007 had no significant variation in *Elymus* cover with planting density, and the cover was very low at all planting densities (Fig. 1I).

Cover of non-native species in year 3 varied significantly with planting density, planting year, and their interaction (Table 1). Non-native cover generally decreased with increasing planting density in plots planted in 2005 and 2006 (Fig. 1J & 1K). In contrast, non-native cover did not vary significantly among planting density treatments in plots planted in 2007, and the cover was relatively high at all planting densities (Fig. 1L).

Long-Term Dynamics

At the end of the study (2009), planting years with high emergence (2005 and 2006, Fig. 1A & 1B) had *Elymus* cover greater than that of all non-native species combined (Fig. 2A & 2B; means averaged across all treatments). In contrast, 2007, which had relatively low emergence (Fig. 1C), produced *Elymus* cover that was a fraction of that of non-native species (Fig. 2C). Similarly, the trajectories of covers over three growing seasons was for *Elymus* dominance in plots planted in 2005 and 2006, but for non-native dominance in plots planted in 2007. The most common non-natives were *Salsola kali* (an annual forb), *Sonchus arvensis* (a perennial forb), and *Hordeum jubatum* (a perennial grass).

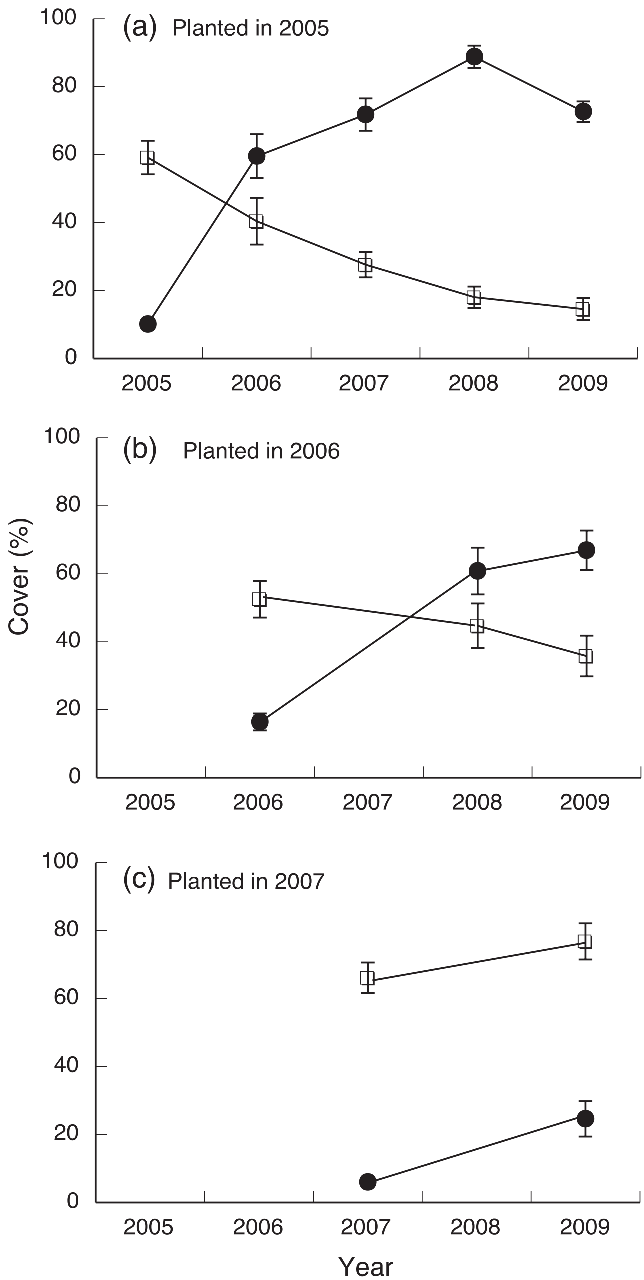

Figure 2. Cover of the native grass *Elymus lanceolatus* (solid circles, mean ± SE) and all non-native species (open squares) over time in three planting years (2005–2007), averaged across all treatments.

Herbivory and Interspecific Neighbors

For plots with herbivory and interspecific neighbors excluded (planted at 1800 seeds/m^2), emergence in year 1 varied significantly among experimental treatments and planting years, but not with the interaction between these factors (Table 2). Pairwise comparisons of treatment means showed that both herbivore exclusion and neighbor removal significantly increased emergence relative to untreated control plots (Fig. 3A–C).

Table 2. ANOVA results for effects of treatment (control, no herbivores, no interspecific neighbors) and planting year on the emergence, establishment and cover of the native grass *Elymus lanceolatus*, and the cover of non-native species (error df = 36).

Source	df	SS	F	p
Emergence				
Treatment	2	0.20	7.72	0.002
Year	2	0.81	31.16	<0.001
T × Y	4	0.09	1.79	0.152
Establishment				
Treatment	2	0.35	4.89	0.013
Year	2	0.61	8.36	0.001
T × Y	4	0.25	1.71	0.169
Native cover				
Treatment	2	0.32	1.25	0.297
Year	2	8.51	33.46	<0.001
T × Y	4	0.14	0.28	0.885
Non-native cover				
Treatment	2	0.18	0.70	0.505
Year	2	2.13	8.06	0.001
T × Y	4	0.71	1.34	0.272

df, degrees of freedom.

Establishment (September density expressed as a proportion of July density) in year 1 varied significantly among experimental treatments and planting years, but not with the interaction between these factors (Table 2). Pairwise comparisons of treatment means showed that establishment was significantly greater in the absence of neighbors than in control plots (Fig. 3D–F). In contrast, herbivore exclusion had no significant effect on establishment.

Cover of *Elymus* in year 3 (i.e. at the end of the third growing season in each year of 3 years of planting) did not vary significantly among experimental treatments (Table 2, data not shown). Cover varied among planting years (means in Fig. 1G–I, for density 1800 seeds/m^2), but not with the interaction between treatment and planting year (Table 2).

Cover of non-native species in year 3 did not vary significantly among experimental treatments (Table 2, data not shown). Cover varied among planting years (means in Fig. 1J–L, for density 1800 seeds/m^2), but not with the interaction between treatment and planting year (Table 2).

Discussion

This 3-year study suggested that poor establishment in years with unsuitable conditions can be overcome by repeated planting over several years, but not by planting high densities of seeds in poor years. Emergence was relatively low in 2007 (Fig. 1C), and after three growing seasons, cover of native grasses was low (Fig. 1I) and cover of non-native species was high (Fig. 1L).

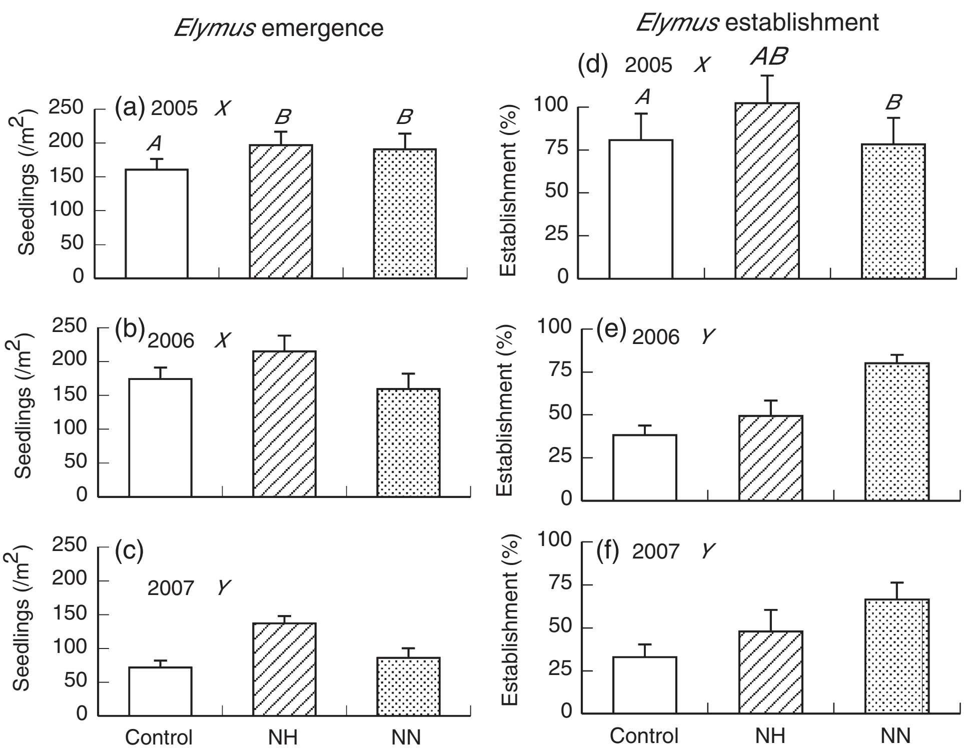

Figure 3. (A–C) Emergence of seedlings (mean + SE) of the native grass *Elymus lanceolatus* in three planting years (2005–2007), planted at 1800 seeds/m^2 in control plots (C), non-herbivore plots (NH) and non-interspecific neighbor plots (NN). Seedling number varied significantly among treatments and planting years (Table 2). *A*, *B*: Means of treatments with different letters are significantly different. *X*, *Y*: Means of planting years with different letters are significantly different. (D–F) Establishment of *Elymus* in early September of three planting years (2005–2007). Seedling number varied significantly among treatments and years.

This was true even for plots planted at high density. In contrast, plots planted in 2005 and 2006 had higher establishment (Fig. 1A & 1B) and greater final cover (Fig. 1B & 1H).

Low germination in 2007 was likely due to low growing-season precipitation, which was only 65% of the 30-year average (Fig. S1). The year 2006 also had low precipitation, but it followed a year with precipitation close to that of the 30-year average. Accordingly, 2005 with near-average precipitation had high germination and establishment, 2006 with low precipitation had high germination but low establishment, and 2007, the second dry year in a row with low precipitation, had low germination and low establishment. Growing-season temperatures may have contributed to these trends, with 2005 being slightly cooler than average, and 2006 and 2007 being slightly warmer. Conditions in 2005 were so favorable that seedlings continued to emerge in July and August, as shown by establishment values greater than 100% only in that year (Fig. 1D). Large among-season variation in soil-available water, driven by precipitation and evaporation, is typical of semiarid grasslands (Knapp & Smith 2001). Water availability is well-known as a driver of regional productivity (McCulley et al. 2005), but it plays a central role in controlling among-year variation in germination (Ambrose & Wilson 2003; Bakker et al. 2003; Blumenthal et al. 2008).

In spite of low germination in 2007, seedling emergence that year did increase significantly with planting density, in the same way as in more favorable years, as shown by the lack of a year × density interaction (Table 1, Fig. 1A–C). Soil moisture in this region is greatest in spring (James et al. 2003; Blumenthal et al. 2008), following snowmelt (note the negative winter temperatures, Fig. S1) and because of the peak of annual precipitation early in the growing season.

Seedling emergence was a very small fraction of planting density even under the most favorable conditions i.e. 10% in 2005. This fits well with a meta-analysis of 27 seed addition studies that found an average germination rate of 14% (Clark et al. 2007), suggesting that small-scale environmental factors such as safe sites influence seedling success even under favorable conditions.

In contrast to emergence, establishment showed a significant interaction between year and density (Table 1, Fig. 1D–F), because establishment decreased with increasing density in the most favorable planting year (2005) but not in the least favorable year (2007). This suggests that in the favorable year (2005), high establishment at high planting densities resulted in intraspecific competition and self-thinning (Ladd & Facelli 2005). On the other hand, 2007 with low emergence showed no influence of density on establishment i.e. no self-thinning. Grasses planted at 1900 seeds/m^2 elsewhere, in the Great Basin, showed no self-thinning (Huber-Sannwald & Pyke 2005).

Most relevant to long-term outcomes, the cover of *Elymus* after three growing seasons also showed a significant interaction between year and density (Table 1, Fig. 1G–I). In the most favorable planting year (2005), cover increased with planting density, whereas in the least favorable year (2007), it did not. Increasing seed density (977–1557 seeds/m^2) in Montana also increased native grass density, but this effect persisted after 3 years only for one of three study species (Sheley et al. 2006).

Elymus cover after three growing seasons in favorable years was maximized (i.e. not significantly different from the greatest cover) at planting densities of 300 seeds/m^2 in 2005 and 600 seeds/m^2 in 2006 (Fig. 1G–I). The required initial planting density in 2006 may have been higher because of lower establishment that year. Thus, the most economical process for ensuring success (assuming that seed costs are high and planting and site-preparation costs are low) may be to plant at moderate density (300–600 seeds/m^2) in repeated years until a favorable year is encountered.

Non-native covers after three growing seasons were opposite to those of *Elymus*, with low covers following planting years that were favorable for *Elymus* germination (2005 and 2006) and high covers following the planting year with low *Elymus* germination (2007). Non-native cover after three growing seasons decreased with increasing *Elymus* planting density, but only in favorable years (2005 and 2006), resulting in a significant year × density interaction. Thus, high planting densities in favorable years reduced populations of non-native species, and presumably competition from those populations (Stevenson et al. 1995; Sheley et al. 1999; Bakker & Wilson 2004; Simmons 2005; Carter & Blair 2012). The relatively great importance of planting year to *Elymus* success and the suppression of non-natives is illustrated in Figure 2, which shows means averaged across all planting densities. Favorable planting years (2005 and 2006) show trajectories of native dominance even after three growing seasons. In contrast, the unfavorable planting year (2007) shows a trajectory of non-native dominance.

Communities of non-native species in the experiment were dominated by short-lived, early successional species. Over 18 years, a nearby restoration was dominated by waves of other non-native species, such as the perennial grass *Bromus inermis* and the thistle *Cirsium arvensis* (Wilson & Pinno 2013). These later-successional non-native species might be minimized by high covers of *Elymus* resulting from initially high planting densities (Bakker & Wilson 2004).

Plots with herbivores excluded had significantly greater seedling emergence than controls (Fig. 3), suggesting that herbivores decreased emergence, in accordance with other studies (Howe et al. 2002; MacDougall & Wilson 2007; Orrock et al. 2008; Maron et al. 2012; Drystek & MacDougall 2014). In addition to those studies, we tested for differences among years and found no significant interaction between year and herbivore exclusion, suggesting that herbivory was a constant effect in our three planting years. In contrast to those studies, the reduction of emergence attributable to herbivores was relatively small, 26% averaged among the 3 years, relative to other studies with up to 89% of seeds consumed by granivores (Howe et al. 2002).

In contrast to the effects of herbivore on emergence, establishment was not increased significantly by herbivore exclusion, even though the trend for greater establishment in the absence of herbivores was constant among the 3 years examined (Fig. 3). The more negative effects of herbivores on emergence than on establishment suggests that granivory of seeds is more important than herbivory of seedlings.

Removal of interspecific neighbors significantly increased both germination and establishment of *Elymus* (Fig. 3), as has been noted previously (Bakker et al. 2003). The absence of an interaction involving planting year suggests that neighbors limited *Elymus* in all years regardless of among-year differences in weather.

In summary, seedling emergence and establishment varied strongly among the 3 years of this study, The native grass *Elymus* achieved greater than 50% cover one to 3 year after sowing at densities of 300–600 seeds/m^2 in years with relatively high emergence and establishment, but not following a year of low emergence. Variation in restoration success was addressed by repeated planting, but not by planting at high density. Our results from North America may also apply to grassland restorations in other semiarid regions, such as the Mediterranean (Le Houerou 2000), Australia (Harris et al. 2006) and Africa (Carrick & Krüger 2007), where among-year variation in rainfall is also great.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Mean monthly temperature (A) and total monthly precipitation (B) near the study site during 2004–2009 (the duration of the study and the preceding year). Digits: means during June–August in each of the 3 years in which seeds were planted; italics: June–August means (±SE) for the period 1976–2006.

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