

Annual Cover Crops Do Not Inhibit Early Growth of Perennial Grasses on a Disturbed Restoration Soil in the Northern Great Plains, USA

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ABSTRACT

In agricultural, rangeland, and forest system revegetation projects, cover crops are used for competitive exclusion of weeds and to stabilize soil. Within revegetation projects, annual or short-lived perennial grasses are often sown at the same time as the perennial grasses that are the desired species for long-term landscape rehabilitation. When cover crops are utilized to control weeds, the same principle of competitive exclusion may apply to sown perennial grasses. In this project, we tested if an annual grass cover crop reduces the early stage performance of sown perennial grasses. We conducted four experiments to evaluate the effects of annual cover crops on perennial grasses. The experiments included *ex situ* growth chamber experiments in two soil types, an agronomic soil, and soil collected from a revegetation project in a trenched water pipeline in western North Dakota. We also performed two *in situ* experiments where the presence of annuals was manipulated. Annual cover crops only reduced perennial grass biomass *ex situ* in the agronomic soil. The disturbed pipeline soil was high in sulfur and sodium. Even when this soil was fertilized, annual cover crops did not reduce sown perennial performance. In stressful environments, or when there is natural microenvironmental variability, annual cover crops do not appear to be costly for the early-stage establishment of more long-term, desirable species.

Keywords: *Avena sativa*, facilitation, grassland restoration, gypsum soil

During revegetation activities following a disturbance, an annual or short-lived perennial cover crop is often planted with the desired slower-growing perennial species to exclude weeds, stabilize soil, and ameliorate harsh abiotic conditions. Because plant species often compete for resources, it is possible that annual cover crops may actually reduce early stage establishment and growth of desirable perennial species. Here we evaluate the degree to which annual grass cover crops may be costly for desirable perennial grass species emergence and early growth within a restoration context.

Annual and short-lived perennial cover crops are commonly used for erosion control in agricultural systems (see Lu et al. 2000), but cover crops only sometimes provide this benefit in forest and rangelands after large-scale disturbance, such as fire (Beyers 2004). Annual or fast-growing cover crops are sown to provide immediate products, such as forage for livestock, as perennials mature, although supporting data are mixed (Beyers 2004). Cover crops can exclude weeds in agricultural systems and sometimes in rangeland environments (Lu et al. 2000, Cox and Anderson 2004, but see Sheley et al. 2006, Waitman et al. 2009, and Dickson et al. 2010), although few studies examine potential negative effects on natives from cover crop species.

The results from studies considering the effect on natives from cover

crops are contradictory. In prairie pothole environments, cover crops can have either very limited competitive effects or significant competitive effects on revegetation species (Sheley et al. 2006, Iannone and Galatowitsch 2008). For rough fescue/bluebunch wheatgrass (*Festuca campestris*/*Pseudoroegneria spicata*) assemblages, cover crops either reduced the biomass of revegetation species or had no significant effect (Herron et al. 2001, Sheley et al. 2006). Perennial grass species found in the upper midwestern United States are variable in their response to competition. For example, bluebunch wheatgrass competition sensitivity has been observed in some environments (Herron et al. 2001), but not others (Blank 2010). Two grama species, blue grama and side oats grama (*Bouteloua gracilis* and *B. curtipendula*), have consistently

been shown to respond negatively to neighbors (Peltzer 2001, Grant et al. 2003, Schmidt et al. 2008). We expect species identity and ecological characteristics of the site to play critical roles in the costs and benefits of cover crop seeding. Even though cover crops are widely used, we still lack a mechanistic understanding of factors affecting their benefits and drawbacks.

Disturbed areas that require revegetation may also be stressful and have poor conditions for seed germination and establishment (Call and Roundy 1991). In these stressful conditions, cover crops may act as small-scale ecosystem engineers, creating environments without which other plants may not survive or thrive (Jones et al. 1997, Maestre et al. 2003, Gomez-Aparicio 2009, Maestre et al. 2009). We know that cover crops can shade the soil, increase filtration, improve site fertility, and increase the establishment of desirable plants (Choi and Wali 1995, Lu et al. 2000, Krueger-Mangold et al. 2006). While many studies show that weedy or invasive annual grasses can reduce the performance of perennial grasses (Hamilton et al. 1999, Humphrey and Schupp 2004, Huddleston and Young 2005), these studies do not specifically address cover crops and the stressful conditions that may occur within restoration areas.

Plant-plant interactions can be facilitative or inhibitory at separate life-history stages (Goldberg et al. 2001, Leger and Espeland 2010), while seed-seed interactions can inhibit or induce germination (Dyer et al. 2000, Tielborger and Prasse 2009). Competition among seedlings can reduce plant growth or, alternatively, increase survivorship (Espeland and Rice 2007, Leger and Espeland 2010). Competition is generally thought to be important as plants allocate resources to reproduction (Goldberg et al. 2001). To understand the costs and benefits of cover crops, it is important to examine the effect of plant neighbors at multiple life history stages.

We present here the results of four studies that investigate the impact

of cover crops in a restoration seeding along a buried water pipeline in western North Dakota rangeland on seedling emergence, individual plant growth of perennial grasses, and perennial grass productivity on a per plot or per pot basis. These studies begin to tease out the importance of soil type, ecological variability, and spatial scale in the outcome of interactions between annual cover crops and desirable perennial grasses.

Methods

Study Sites

This study took place in the Northern Great Plains, in a shortgrass/mixed grass prairie community. This vegetation type has only one native annual grass, six weeks fescue (*Vulpia octoflora*), with the remaining vegetation consisting of the exotic annual bromes, cheatgrass (*Bromus tectorum*) and Japanese brome (*Bromus japonicus*) occurring in small, patchy populations. Our study sites included a revegetated pipeline and surrounding areas on a private ranch and a farm. The ranch is located near the Elkhorn Ranch Unit of Theodore Roosevelt National Park in western North Dakota (47° 08'44" N, 103° 47'57" W). It receives 280–380 mm of rainfall per year, falling evenly throughout the year and making the landscape more hospitable to perennial grass and forb species than annuals (NRCS 2006). Average annual temperatures range between 6° and 8° C, and the average freeze-free period is 140 days (NRCS 2006). The farm site, located in Froid, Montana (48° 20' 4" N-104° 29' 46" W), receives 330 mm precipitation per year, with annual temperatures ranging between 5° and 6° C, and a normal freeze-free period average of 135 days (NPARL 2006, NRCS 2006).

In summer 2008, a water pipeline was installed by the North Dakota State Water Commission (NDSWC) throughout the western portion of the state. The pipe was laid in a 2.13-m

deep trench and covered with the removed native soil. The width of the disturbance ranged from 1.5 to 2.5 m. In late May 2009, the NDSWC seeded the disturbed soil with four native perennial species and one annual grass cover crop by rangeland drill at recommended rates of pounds of pure live seed (#PLS) per acre. Seeded species were western wheatgrass (*Pascopyrum smithii*, 8 #PLS/acre), slender wheatgrass (*Elymus trachycaulus*, 5 #PLS/acre), green needlegrass (*Nassella viridula*, 4 #PLS/acre), sideoats grama (*Bouteloua curtipendula*, 2 #PLS/acre), and common oat (*Avena sativa*, 20 #PLS/acre). Although some of the species used in this experiment require cold stratification to break dormancy, this stratification is not normally applied for large-scale restoration initiatives. Millet (*Panicum miliaceum*), an annual grass, also appeared in the seeded area, possibly as a contaminant.

Experimental Protocols

We conducted *ex situ* studies to examine the effect of soil (agronomic or rangeland) on plant-plant interactions. We determined if interactions occurred between functional groups (annual cover crop and perennial grasses) as well as if intraguild interactions within perennial grasses were important. In addition, two *in situ* studies were conducted. The first was executed in large plots within the pipeline to determine if competition affects productivity at the field scale. If annual cover crops impede perennial grass growth in this environment, removal of these annual plants early in the growing season should result in compensatory growth in the desirable perennial grasses and result in greater productivity. The second *in situ* experiment was conducted in small plots designed to test if plant-plant competition could be occurring at the small scale, even if it might not be evident at the field scale. Because competition is hypothesized to change as the stress of the environment increases (Goldberg et al. 1999), this experiment was conducted at multiple sites with differing levels of soil stress.

Table 1. Summary of treatments and scales of the four experiments used to examine the effects of cover crop on native perennial grasses, Northern Great Plains, U.S., 2009–2011. The 2009 *ex situ* experiment examined the effects of cover crops on natives between agronomic and pipeline soils. The 2009 *in situ* experiment determined if perennial grasses experienced compensatory growth after the removal annual grass cover crops under restoration conditions. The 2010 *ex situ* experiment examined the effects of cover crops on natives between fertilized agronomic and fertilized pipeline soils. The 2011 *in situ* experiment examined the effects of cover crops on emergence and early growth of perennial grasses under restoration conditions at multiple sites.

Experiment	Perennial grass species	Treatments	Soils	Replication	Plot/pot size	Duration
2009 <i>ex situ</i>	prairie sandreed, western wheatgrass, wideoats grama, blue grama	Factorial: 1) Low/high density perennials 2) With/without annuals	1) Pasteurized farm 2) Unpasteurized pipeline	6–7	8.75 × 8.75 × 8.75-cm pots	13–14 weeks
2009 <i>in situ</i>	western wheatgrass, slender wheatgrass, green needlegrass, sideoats grama	1) no annuals 2) with annuals	Untreated pipeline	5	200-m ² plots	12 weeks
2010 <i>ex situ</i>	western wheatgrass, slender wheatgrass, green needlegrass, blue grama	Factorial as above	1) Unpasteurized/fertilized farm 2) Unpasteurized/fertilized pipeline	3	8.75 × 8.75 × 8.75-cm pots	6 weeks
2011 <i>in situ</i>	western wheatgrass, slender wheatgrass, green needlegrass, blue grama	Factorial as above	1) Untreated farm 2) Untreated pipeline	8–40	12.6-cm ² plots	9 weeks

We conducted *ex situ* and *in situ* experiments using similar, but not identical, mixes of perennial grasses (Table 1) to qualitatively examine the effect of species composition on our results. Parallel to the seeds used in the restoration, we used purchased materials as our seed source. Our experiments varied in duration from 6–22 weeks (Table 1), in accordance with the typical growing season of annual grasses. In each of the experiments where density of perennial grasses was manipulated, the low density treatment roughly approximated the recommended seeding rate used in the revegetation.

The 2009 *ex situ* experiment tested whether competition that is typically observed among plants in well-watered conditions using pasteurized, agronomic soil would also be observed under well-watered conditions in an untreated soil collected from the restoration area. To address this question, a four-way factorial competition design of two densities of perennial grasses with or without annual cover crops (Table 1) was planted in two soil types. The first soil (Williams loam, hereafter referred to as the *agronomic* or *farm*

soil) was collected from a 2.1 × 6 × 0.1 m deep area on an unsprayed section of the farm and pasteurized. The second soil was an untreated rangeland soil (Cabbart-Badland complex) collected at three locations spanning 3 km along the seeded pipeline. The soils were homogenized and placed into pots (8.75 × 8.75 × 8.75 cm). We then seeded plants in four densities into the pots: LDP (Low Density Perennial: 1 seed each of perennial grass species), LDA (Low Density with Annuals: 1 seed each of perennial grass species with 2 seeds of common oat and 2 seeds of millet), HDP (High Density Perennial: 2 seeds each of 4 perennial grass species), and HDA (High Density with Annuals: 2 seeds each of 4 perennial grass species with 2 seeds of common oat and 2 seeds of millet). We planted each pot with all four perennial grass species. We planted six replicates per perennial-only treatment, and seven replicates of annual treatments because of space constraints and because we expected greater variability in the annual treatments. The perennial grass species we used in this experiment were prairie sandreed (*Calamovilfa longifolia*),

western wheatgrass, blue grama, and side oats grama. We randomly assigned pots to blocks for a fully replicated block design. We then placed the experiment in a growth chamber with 12-hour days at a high temperature of 27°C and a low of 3°C to mirror May temperatures in the region. One month later, we increased the chamber settings to 26°C days and 11°C nights and watered pots as needed. We harvested aboveground biomass by block after 13 to 14 weeks of growth.

We conducted a 2009 *in situ* thinning experiment to determine if annual grass cover crops suppress early growth of perennial grasses under restoration conditions, looking for compensatory growth in perennial grasses once annual cover crops were removed from large plots within the restoration area. We installed 24 large plots (100 m long and spanning the width of the seeding) in July 2009 at the pipeline. These plots were spatially separated into 3 blocks, with 6 km separating the furthest blocks. Within each block, we completely removed annual grasses from 4 randomly-located plots via hand-pulling and left 4 randomly-located plots undisturbed. We then

Table 2. Soil properties of soil types used in (a) 2010 *ex situ* experiment and (b) 2011 *in situ* experiment, Northern Great Plains, U.S., 2009–2011. Value for N is nitrate only, P is strong Bray P, and K, Ca, and Na are neutral ammonium acetate exchangeable.

Location Soil type	(a)		(b)						
	<i>Ex situ</i> Farm	<i>Ex situ</i> Pipeline	Farm Farm	Ranch, Location 1			Ranch, Location 2		Ranch, Location 3
				Grassland	Pipeline	Grassland	Pipeline	Grassland	Pipeline
Texture	Sandy loam	Clay loam	Sandy loam	Sandy loam	Clay loam	Clay loam	Clay loam	Silt loam	Silt loam
pH	7.5	8	5.8	8	8.1	7.9	8	8	8.2
N (mg/kg)	41	27	10	1	8	8	4	1	6
P (mg/kg)	47	10	60	6	7	12	10	19	13
K (g/kg)	0.26	0.23	0.35	0.14	0.19	0.25	0.21	0.12	0.17
Ca (g/kg)	2.22	2.97	1.47	2.97	3	3.66	2.96	2.69	2.94
Na (mg/kg)	44	324	9	16	92	11	18	26	66
S (mg/kg)	20	363	10	14	61	13	15	12	24

harvested aboveground biomass of seeded perennial grasses after 12 weeks from 5 randomly located 20 × 50-cm quadrats in each plot.

In the 2010 *ex situ* experiment, we examined whether the outcome of competition between annual cover crops and desirable perennial grasses was the same when soils were collected from different locations with similar nutrient status and differences in soil texture (Table 2a). We followed the same protocols as the 2009 *ex situ* experiment, and we also applied 59 mL of Peterson’s 20-20-20 fertilizer at 16 g/L (1:15) to each pot at the start of the experiment and after 3 weeks. Each application resulted in approximately 117 mg N, 77.3 mg P, and 147 mg K added per pot—enough for pots with pipeline soil to reach an equivalent nutrient status to farm soil. The perennial grass species we used in this experiment were western wheatgrass, slender wheatgrass, blue grama, and green needlegrass. We harvested biomass after 6 weeks of growth. The shorter time scale of this experiment was so that annual and perennial grass belowground biomass could be separated because in the 2009 *ex situ* experiment, roots were too compacted for these data to be collected. We dried and weighed biomass (both leaf and root) of each functional group per pot and analyzed pre-fertilized samples from the bulked soil used in this experiment for nutrients and texture (Table 2a).

To determine if annual grass cover crops affect emergence and early growth of perennial grasses in plant-plant interactions under field conditions, we conducted the 2011 *in situ* seeding experiment using the same seeded species and seed numbers as the 2010 *ex situ* experiment. The experiment was established at the ranch site as well as the farm site (Table 1) in small, 12.6-cm² plots. In May 2011, we established 40 plots at the farm site in a 1 × 3-m area. At the ranch location, we located 3 blocks within the pipeline and 3 in the adjacent intact grassland with 8 replicates of each seeding treatment within each block (Table 1). Blocks were separated by 2 to 3 km. Millet did not germinate in this experiment. We harvested biomass from the ranch and farm locations in July. Severe spring and summer rains washed away all the established plots on the pipeline, but only some of the farm and grassland plots were affected. We collected ten 6 cm diameter × 6 cm deep soil samples from each pipeline grassland block and from the farm and prepared composite samples by block for nutrient and texture analysis (Table 2b).

For each seeded experiment (2009 *ex situ*, 2010 *ex situ*, and 2011 *in situ*), we measured emergence (the percent of seeds that made the transition from seed to the seedling stage). In all experiments, we quantified total leaf biomass produced by perennial grasses produced in each experimental unit (pot or plot). Total leaf biomass

indicates the effects our treatments might have on vegetative cover, which is one indicator of successful restoration. Total leaf biomass of perennial grasses is dependent on emergence; with more plants having emerged, we would expect more biomass to be produced, regardless of any competitive or facilitative effects that occur during seedling growth. Because our treatments were expected to affect emergence, we calculated the leaf biomass per emerged individual perennial grass plant to determine how competition or facilitation during growth (decoupled from emergence) affected perennial grass biomass. The biomass of each individual plant indicates its ability to translate resources into biomass and is an indicator of its competitive ability (Tilman 1990). In the 2010 *ex situ* experiment, we collected root biomass data for perennial grasses and used it to calculate both the per plant root biomass and the total root biomass of this functional group for each pot.

Statistical Analysis

We analyzed our data using general linear models with restricted maximum likelihood methods with standard least square means in JMP v. 8.0 (SAS Institute, Cary, NC). A *p*-value < 0.05 was considered significant. All dependent variables except emergence were square root transformed to condition residuals. After transformation, normality of data was tested with Shapiro-Wilk’s *W* test. All transformed

variables had close to normal distributions ($W > 0.79$, $p < 0.05$), with the exception of emergence in the 2009 *ex situ* experiment ($W > 0.6$, $p < 0.05$). For the *ex situ* experiments, we measured treatment effects on arcsine transformed emergence percentages. The statistical model for emergence included soil, annuals (present or absent), sown perennial density (high or low), annuals*soil interaction, and density*soil interaction. Annuals germinated in every experimental unit in which they were sown, so our treatment identification of annuals (Y/N) was accurate for all plots and pots as planted even though millet did not germinate in the 2011 *ex situ* experiment. Our model for measures of biomass was biomass = soil, annuals (Y/N), number of emerged perennials (continuous variable), and annuals*soil interaction. We used this full model when the dependent variable was biomass per plant. However, when performance was measured as total biomass per pot (or plot) we excluded number of emerged perennials from the model. We did not test three-way interactions. To examine compensatory growth (2009 *in situ* experiment), we modeled the effects of block (random factor) and annuals (present or absent) and their interaction (block*annuals) on total leaf biomass of perennials in the sample plots. In our 2011 *in situ* experiment, because of the uneven distribution of plots destroyed in 2011 by severe weather, we were unable to include block in our analyses. When a significant two-way interaction was found, differences among means were compared using Tukey's HSD, with a significance value set at $p = 0.05$. Because, in one case, the GLM analysis showed a significant interaction and no differences among means were found using Tukey's HSD, we performed a Student's t-test to determine significant differences among means. Student's t is less conservative than Tukey's HSD as it does not control for multiple comparisons.

Table 3. Results of significant general linear models on perennial grass performance, Northern Great Plains, U.S., 2009–2011. Significant independent variables are shown in bold.

	DF	Sum of Squares	F Ratio	Prob > F	Power
2009 <i>ex situ</i>					
EMERGENCE					
Soil	1	0.351	6.271	0.016	0.33
Annuals	1	0.266	4.757	0.034	0.14
Density	1	0.278	4.980	0.031	0.14
Annuals*Soil	1	0.092	1.651	0.205	0.09
Density*Soil	1	0.029	0.511	0.478	0.05
PER PLANT LEAF BIOMASS					
# Perennials	1	0.001	0.038	0.849	0.27
Soil	1	0.066	5.309	0.042	0.20
Annuals	1	0.020	1.590	0.233	0.64
Annuals *Soil	1	0.019	1.521	0.243	0.06
TOTAL LEAF BIOMASS					
Soil	1	10.207	11.433	0.005	0.14
Annuals	1	0.116	0.130	0.724	0.86
Annuals *Soil	1	6.809	7.627	0.017	0.06
2009 <i>in situ</i>					
PER PLANT BIOMASS					
Location (DF den)	32.2	(t-ratio)	-2.54	0.016	0.77
Annuals	1		2.059	0.154	0.30
Annuals*Location	1		0.0473	0.828	0.06
2010 <i>ex situ</i>					
PER PLANT LEAF BIOMASS					
# Perennials	1	0.001	0.001	0.990	0.06
Soil	1	0.097	7.080	0.016	0.97
Annuals	1	0.030	2.198	0.156	0.41
Annuals *Soil	1	0.536	3.916	0.063	0.52
PER PLANT ROOT BIOMASS					
# Perennials	1	0.0216	1.956	0.180	0.26
Soil	1	0.027	2.489	0.133	0.61
Annuals	1	0.042	3.782	0.069	0.54
Annuals *Soil	1	0.050	4.554	0.048	0.67
TOTAL LEAF BIOMASS					
Soil	1	0.228	5.365	0.032	0.98
Annuals	1	0.023	0.542	0.471	0.41
Annuals *Soil	1	0.035	0.836	0.372	0.41
TOTAL ROOT BIOMASS					
Soil	1	0.059	2.817	0.110	0.70
Annuals	1	0.080	3.810	0.066	0.70
Annuals *Soil	1	0.105	5.045	0.037	0.67
2011 <i>in situ</i>					
EMERGENCE					
Density	1	0.166	1.949	0.167	0.31
Location	1	0.378	4.432	0.039	0.41
Annuals	1	0.017	0.205	0.652	0.05
Annuals * Location	1	0.047	0.549	0.461	0.08
PER PLANT LEAF BIOMASS					
# Perennials	1	0.002	1.088	0.301	0.20
Location	1	0.019	11.594	0.001	0.78
Annuals	1	0.001	0.505	0.480	0.07
Location* Annuals	1	0.004	2.630	0.109	0.36

Results

In the 2009 *ex situ* experiment, soil, presence of annuals, and perennial grass seed density all affected emergence (Table 3a). Although all four species emerged, percentages were low (Table 4a), with blue grama having the highest emergence ($19\% \pm 38\%$ SD) and side oats grama having the lowest emergence ($2\% \pm 10\%$). The presence of annuals reduced emergence slightly (Table 4a), while higher density sowings of perennial grasses more than doubled the emergence percentage (Table 4a). Soil type was a main effect and its interaction with the presence of annuals affected the total leaf biomass of perennials in each pot, and per plant leaf biomass was affected only by soil (Table 3a). Per plant leaf biomass was exponentially lower in pipeline soil than in farm soil (Table 4b). Perennials produced the most leaf biomass on farm soil where annuals were not present (Figure 1). When annuals were present on the farm soil, the leaf biomass produced by perennials was indistinguishable from the production on pipeline soil (Figure 1).

In the 2009 *in situ* experiment to test whether annuals suppressed growth of perennial grasses within the pipeline, leaf biomass of perennial grasses in each plot was not affected by the removal of the annual cover crop ($F_{1, 23} = 2.04, p > 0.16$).

In the 2010 *ex situ* experiment where plant performance in the fertilized, untreated soil from the farm and pipeline were compared, no significant treatment effects on emergence ($F_{1, 23} = 0.23, p > 0.6$) were found. All four perennial grass species emerged, with slender wheatgrass having the highest emergence ($85\% \pm 32\%$) and green needlegrass having the lowest emergence ($2\% \pm 10\%$). Western wheatgrass had the next-lowest emergence in this experiment at $42\% \pm 46\%$. The main effect of soil was significant for leaf biomass (total and per plant, Table 3b), which was greater on farm soil compared to pipeline soil (Table 4b).

Perennial grass plants were twice as large when grown in farm soil, which resulted in more than 100% greater aboveground productivity of perennial grasses in these pots. The interaction between soil type and presence of annuals was significant for root biomass (total as well as per plant, Table 3b). In the absence of annuals, farm soils supported more belowground production by perennial grasses than the other treatments (Figures 2a and 2b). Per plant belowground biomass was not statistically different among treatments when Tukey's test was performed, but the Student's *t*-test shows that the pattern of belowground biomass per plant is statistically similar to belowground total biomass across treatments.

In the 2011 *in situ* seeding experiment, location affected emergence (Table 3c), which was lower at the farm ($38\% \pm 16$) than in the grassland ($54\% \pm 29$). Per plant leaf biomass was less in the grassland site (0.012 g/plant) than the farm site (0.016 g/plant, Table 3c). Total perennial grass leaf biomass per plot was not different among treatments or locations ($F_{3, 73} = 1.03, p > 0.3$). In further *post hoc* analysis of this experiment using only grassland plots, we found no differences in productivity among blocks ($F_{2, 40} = 0.77, p > 0.4$).

Discussion

Our hypothesis that annual cover crops would limit establishment and growth of native perennial species was supported in *ex situ* farm soils. In the controlled environment in farm soil, annual cover crops competed with perennial grasses, which may be due to the removal of beneficial mycorrhizal species via pasteurization. Annual grass species benefit less than perennial grass species from mycorrhizal fungi (Wilson and Hartnett 1998). The hypothesis of negative competitive effects of cover crops on perennial grasses was not supported in *ex situ* pipeline soil or any *in situ* experiment, including one performed in farm soil.

Under most conditions, annual cover crops did not compete with perennial grasses.

Even in fertilized pipeline soil in containers where water was plentiful, the presence of the annual cover crop did not affect perennial grass growth. This was surprising as annual cover crop individuals were quite large compared to the perennial grasses. The pipeline soil was high in sodium and sulfur (Table 2a), which may have stressed these plants, regardless of the fertilization treatment. Although not statistically significant, perennial biomass in the pipeline soil tended to be higher when annuals were present (Figures 2a and 2b, Table 4c). This may have been due to a facilitative effect of soil shading, with increased water availability making up for the salinity stress in this soil type (Table 2). Competition may be less important in stressful environments, with plants limited in their capacity to gain resources so that they cannot pre-empt them from neighbors (Goldberg et al. 1999). Additionally, of course, if densities of annual cover crops had been even higher, we may have seen a negative effect. Because pots were root bound at the end of our first experiment, we conclude that the scale of our *ex situ* experiments was appropriate to force plant-plant interactions.

The power of some of our experiments was quite low (Table 3), yet restoration projects often contain thousands of individual plants. We have therefore reported treatment means for emergence and individual plant growth (Table 4c). Cover crops may have stimulated emergence (pipeline soil in the 2009 *ex situ* experiment, and in farm soil in the 2011 *in situ* experiment), and individual plants may have been bigger with annuals present (in pipeline soil in both *ex situ* experiments, in locations 1 and 3 in the 2009 *in situ* experiment, and in farm soil in the 2011 *in situ* experiment) if our sample size had been greater. Of the 15 comparisons we could make in Table 4c, seven show

Table 4. Means for perennial grass (a) emergence by significant main effects for the 2009 *ex situ* experiment, (b) leaf biomass separated by the significant main effect of soil/site in the *ex situ* experiments and the 2011 *in situ* experiment, and (c) emergence and leaf biomass per plant by soil/site and annual presence, Northern Great Plains, U.S., 2009–2011. For a–b, all means significantly different within experiments ($p < 0.05$). Non-transformed means are shown (\pm SD).

a)

Soil	% Emergence	Annuals	% Emergence	Density	% Emergence
Farm	13 (17)	No	11 (17)	High	13 (17)
Pipeline	5 (14)	Yes	8 (16)	Low	6 (15)

b)

	Farm	Pipeline
2009 <i>ex situ</i>		
leaf biomass per plant (mg)	21.9 (14.9)	1.8 (2.2)
2010 <i>ex situ</i>		
leaf biomass per plant (mg)	9.8 (10.8)	4.6 (3.4)
total leaf biomass (mg)	25.7 (27.6)	9.3 (8.3)
2011 <i>in situ</i>		
leaf biomass per plant (mg)	1.6 (1.2)	1.2 (1.4)

c)

	Soil	Pipeline		Farm			
	Annuals	No	Yes	No	Yes		
2009 <i>ex situ</i>							
Emergence (%)		2 (7)	8 (19)	21 (19)	7 (13)		
Leaf biomass per plant (mg)		1.1 (0)*	2.5 (2.0)	28.6 (11.7)	8.6 (11.6)		
2010 <i>ex situ</i>							
Emergence (%)		44 (25)	44 (15)	45 (21)	19 (23)		
Leaf biomass per plant (mg)		2.3 (1.3)	4.2 (6.3)	16.3 (13.5)	5.2 (5.5)		
	Site	Location 1		Location 2		Location 3	
	Annuals	No	Yes	No	Yes	No	Yes
2009 <i>in situ</i>							
Leaf biomass per plant (mg)		4.9 (4.0)	8.0 (7.1)	6.1 (7.2)	4.6 (3.9)	2.6 (2.6)	4.5 (4.3)
	Site	Grassland		Farm			
	Annuals	No	Yes	No	Yes		
2011 <i>in situ</i>							
Emergence (%)		59 (32)	48 (23)	36 (15)	46 (18)		
Leaf biomass per plant (mg)		1.4 (1.8)	0.1 (0.1)	1.5 (1.2)	2.2 (1.4)		

*Only one plant emerged in this treatment combination.

a potential benefit of the presence of cover crops and seven show a potential cost. Four of the costly seven occur in farm soils in *ex situ* experiments, giving further support to the hypothesis that cover crops are more costly to perennial grass growth and establishment in nonstressful environments. Additional research on the effect of cover crops on desirable species performed across soil stress gradients is clearly needed.

It is important to consider evolutionary history when delineating environments as stressful or non-stressful

(Bijlsma and Loeschcke 2005, Espeland and Rice 2007). The soil in the pipeline had high sodium levels (Table 2a). While a salty soil may be stressful for plants not adapted to these conditions, halophytic species may not experience stress in salty soils. Individuals from halophytic species have been shown to be affected by competition in saline environments (Badger and Unger 1990). The genotypes sown in this experiment were commercially available, general purpose genotypes. If the materials sown in this experiment had been adapted

to salty soil, we may have observed more competition.

Soil type, site, and the presence of annuals did not consistently affect emergence in these experiments. Some of this inconsistency could be due to differing levels in seed viability (which we did not test) among our study species. Because we used slightly different species mixes among our experiments, if each species had a different percent viability this would change our emergence results among experiments. The 2009 *ex situ* experiment had a different species mix than the 2010 *ex situ*

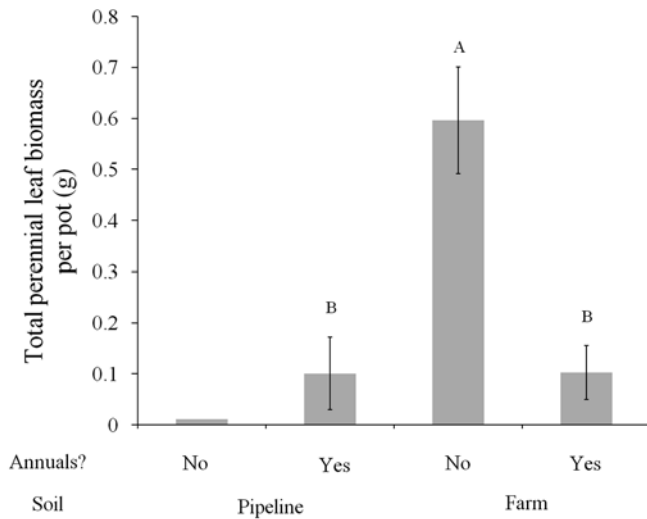


Figure 1. Results of 2009 *ex situ* experiment, Northern Great Plains, U.S. Presence of annuals reduces total perennial grass leaf biomass per pot on farm soil. Bars are one standard error, and different letters indicate significant differences between means (Tukey's HSD; $p < 0.05$).

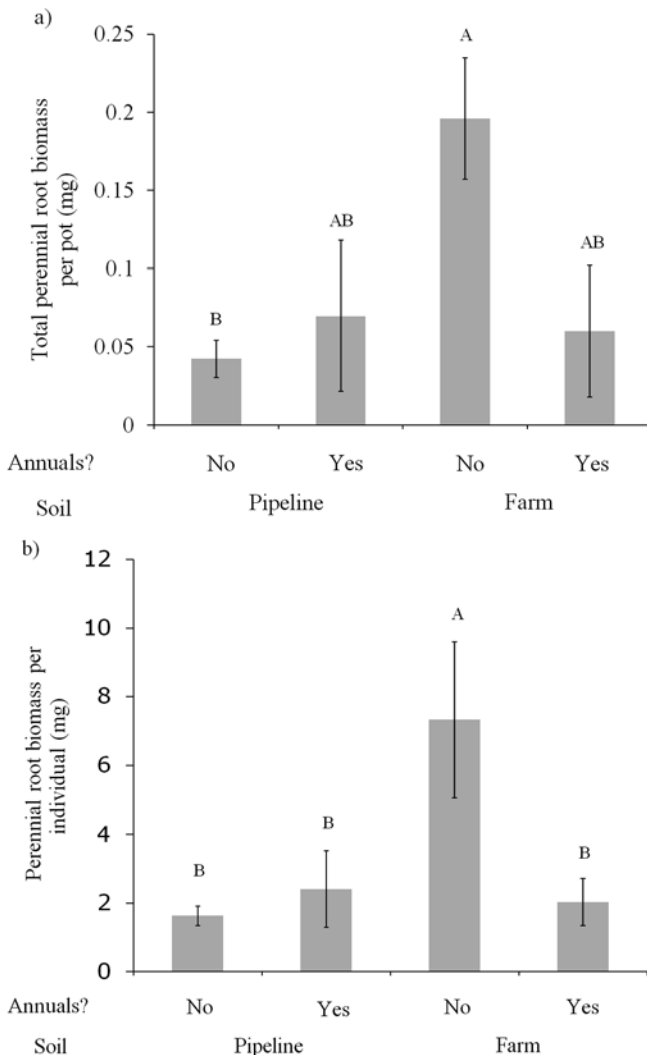


Figure 2. Total root biomass per pot (a) and root biomass per plant (b) for perennial grasses in the 2010 *ex situ* experiment, Northern Great Plains, U.S. Bars are one SE. Different capital letters indicate significant differences (a. Tukey's HSD; $p < 0.05$. b. Student's *t*; $p < 0.05$).

and 2011 *in situ* experiments. In the 2009 *ex situ* experiment, perennials in farm soil had greater emergence than perennials in pipeline soil. In the 2011 *in situ* experiment, grassland locations had greater emergence than farm locations, but the same species mix in the 2010 *ex situ* experiment, using the same seed lots, showed no effect of soil on emergence. This 2010 *ex situ* experiment did show a slight inhibitory effect of annual presence on perennial emergence, an effect not seen in the 2011 *in situ* experiment. It is possible that this result is due to the annual species composition differing among these experiments: in the 2010 *ex situ* experiment, millet seed germinated, but in the 2011 *in situ* experiment, millet did not germinate and we presume it was inviable. Common oat was present in both experiments. These results suggest that a variety of factors determine emergence of perennial grasses, and some of the factors that we did not control for (i.e. temperature across years, seed age, species composition, seed viability, and climate) and their interactions are likely greater or more consistent determinants of emergence than the presence of annuals, soil type, or intraguild density (Fowler 1986, Humphrey and Schupp 1999).

Because competition may be more important in non-stressful sites compared to stressful sites (Goldberg et al. 1999), grassland sites adjacent to the pipeline were added to the experiments in 2011 to test if the less stressful soil in grassland sites might affect competitive interactions among guilds. We hypothesized that if grassland soil was less stressful than pipeline soil, then we might observe competition between the annual cover crop and perennial grasses at grassland sites. Although severe weather destroyed the pipeline plots, making direct comparisons of competitive interactions impossible, we observed that soil collected from the pipeline tended to have higher pH and more S and Na than the grassland soils (Table 2b). The disturbance of trenching the pipeline likely mixed the

soil horizons and changed soil properties making them less hospitable for plant growth. Since we did not observe competition at presumably less stressful grassland sites, we would likely not have observed competition in the pipeline if our plots had persisted.

Seedling growth in perennial grasses was not significantly affected by the presence of annuals in any *in situ* experiment or in *ex situ* tests using pipeline soil. Our results agree with the work of others that show that the presence of an annual cover crop can reduce the performance of desirable revegetation species in some environments but not in others (Herron et al. 2001, Sheley et al. 2006, Waitman et al. 2009). Our results indicate that when the environments are stressful or variable, annual grass cover crops often do not inhibit the early establishment and growth of perennial grasses.

Annual grass cover crops are generally planted for their purported benefits over larger spatial scales: cover crops may reduce runoff (Lu et al. 2000), provide forage (Dhar 1994), or competitively exclude weeds in some environments (Perry and Galatowitsch 2003). Our results show that annual cover crops may not be costly for early perennial grass establishment and growth in stressful environments.

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