

Seed source impacts germination and early establishment of dominant grasses in prairie restorations

M. Kate Gallagher^{1,2,3*} and Stuart Wagenius³

¹Department of Ecology and Evolutionary Biology, University of California, 321 Steinhaus Hall, Irvine, CA 92697-2525, USA; ²Program in Plant Biology and Conservation, Northwestern University, 2205 Tech Drive – Hogan 6-140B, Evanston, IL 60208, USA; and ³Division of Plant Science and Conservation, Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022, USA

Summary

1. Land managers choose seed from a variety of provenances for restoration projects. By selecting seed of the local ecotype, managers can increase establishment in the short term and prevent the disruption of local adaptations and genetic swamping in the long term. However, local seed may be disadvantageous if populations are inbred or maladapted to managed restoration environments. Seed selection may be further confounded by propagation methods.

2. Three dominant C₄ grasses, *Andropogon gerardii*, *Bouteloua curtipendula* and *Sorghastrum nutans*, from three types of seed provenances (remnant, restoration and nursery) were planted as seeds and plugs into experimental plots at three established tallgrass prairie restorations in western Minnesota, USA. Using a common garden design, we tested whether (i) provenance and (ii) site of planting influence germination and first-season survival and growth both (iii) for seeds directly planted in the field and for transplants (plugs).

3. Seed provenance impacted germination and seedling survival in all cases, except *S. nutans* seeded directly in the field. *Andropogon gerardii* and *B. curtipendula* nursery seedlings were consistently taller than those of the other provenance types.

4. When directly seeded, germination, survival and vigour differed among restoration sites; however, the results were species specific. *Sorghastrum nutans* germination varied among sites depending on provenance, indicating that this species may be particularly sensitive to environmental conditions.

5. Germination was 3–12 times greater for plugs than for seeds directly planted in the field in summer, but mortality after planting in the field was low for both groups.

6. *Synthesis and applications.* Provenance and restoration site had varying effects among species, indicating that the dominant C₄ grasses used in this study ought not to be considered ecological equivalents. While we found little evidence of local adaptation, use of local remnant seeds diminishes the risk of spreading maladapted genotypes. Germination limited establishment when sowing seeds directly in summer. Supplemental use of plugs may increase species diversity in restorations.

Key-words: *Andropogon gerardii*, *Bouteloua curtipendula*, C₄ grasses, common garden, local seed, prairie restoration, *Sorghastrum nutans*, tallgrass prairie

Introduction

Among the world's terrestrial biomes, temperate grasslands and savannas are among the most threatened due to extensive habitat loss and human development (Hoekstra

et al. 2005). In North America, the once widespread tallgrass prairie has been reduced by more than 99%, leading to efforts to protect remaining parcels and create restored prairie habitat (Samson & Knopf 1994). Although restoration techniques have become increasingly sophisticated, the extent to which land managers should consider the provenance of their source materials remains an area

*Correspondence author. E-mail: mkgallag@uci.edu

of debate (e.g. Sackville Hamilton 2001; Wilkinson 2001; McKay *et al.* 2005; Vander Mijnsbrugge, Bischoff & Smith 2010).

One common recommendation is that plant materials should be of 'local' ecotypes, sourced from remnant populations as close to restoration sites as possible (Lesica & Allendorf 1999; McKay *et al.* 2005; Vander Mijnsbrugge, Bischoff & Smith 2010). Adaptive genetic and morphological differentiation among ecotypes has been documented in numerous plant species, including some prairie grasses (Clausen, Keck & Heisey 1941; Gustafson, Gibson & Nickrent 2005; Bischoff *et al.* 2006; Hereford 2009). Therefore, using locally sourced seed for restorations may preserve genes adapted to local conditions (Lesica & Allendorf 1999; Sackville Hamilton 2001; Rogers & Montalvo 2004), whereas introducing non-local genotypes may dilute genes associated with local adaptation and disrupt co-adapted gene complexes, both at the restoration site and in surrounding remnants via introgression (Hufford & Mazer 2003).

Using seeds of non-local ecotypes, however, may be desirable if local populations suffer from low genetic diversity (Lesica & Allendorf 1999; Wilkinson 2001). Reduced capacity to adapt to environmental changes is an important cause of extinction, and the rate at which populations adapt depends in part on their genetic diversity (Etterson & Shaw 2001; Reed & Frankham 2003; McKay *et al.* 2005; Hereford 2009). If local populations are genetically depauperate, non-local ecotypes may provide novel genetic material needed for adaptation (Frankel & Soule 1981; Hufford & Mazer 2003; McKay *et al.* 2005).

Concerns about preserving local adaptation, enhancing genetic diversity and avoiding introgression of non-local genes into remnant populations have practical implications for prairie restorations. Prairie grasses regulate ecosystem function, support native species diversity and suppress invasive non-native species (Baer *et al.* 2004; Middleton, Bever & Schultz 2010; Wilsey 2010; Gibson *et al.* 2013). Maladaptations in the ecological properties of a dominant species may have cascading effects through the community (Rogers & Montalvo 2004). The choice of dominant grass seeds used in restoration projects may be crucial to fostering healthy ecosystems, both at project sites and in surrounding remnants (Lesica & Allendorf 1999; Kramer & Havens 2009); yet seed choice practices vary widely (Schramm 1990; Sedivec *et al.* 2009; Johnson *et al.* 2010).

This variation in seed choice practices likely stems, at least in part, from ambiguity among scientists and policy-makers in interpreting exactly what 'local' means (Johnson *et al.* 2010; Vander Mijnsbrugge, Bischoff & Smith 2010). When choosing seed for restorations, land managers are urged to consider source characteristics such as the distance between site of origin and restoration site, the degree of population differentiation and similarity

between habitats. Attempts to determine optimal seed collection zones based on these characteristics, however, have met with mixed success (Hufford & Mazer 2003; Moncada *et al.* 2007; Johnson *et al.* 2010). In heterogeneous environments, neither distance nor ecoregion may be the best gauge of local adaptation (Moncada *et al.* 2007; Bischoff, Steinger & Müller-Schärer 2010; Seifert & Fischer 2010).

Considerations of distance and habitat similarity between the site of origin and restoration site may be further confounded by variation in seed collection and propagation methods. Land managers may collect seed from wild populations, from existing restorations or from propagation fields, the latter two of which may have been seeded with locally or non-locally sourced materials and are likely under different selection pressures than wild populations. Plants cultivated in propagation fields over multiple generations may adapt to cultivation conditions, including low competition and high resource availability (Baisey, Fant & Kramer 2015). They may lose important genetic variation (Aavik *et al.* 2012). Moreover, important life-history traits, including seed dormancy and germination rate, may be altered (Schröder & Prasse 2013), due to both drift and unintended selection (i.e. harvest date and technique, selection for larger seeds, seed cleaning; reviewed in Vander Mijnsbrugge, Bischoff & Smith 2010).

The extent to which land managers should consider provenance of source materials, therefore, is far more complex than simply collecting 'local' ecotypes from wild populations. For each restoration project, managers must consider distance, habitat similarity and propagation methods to assess genetic appropriateness of seed provenances: wild remnants, local restorations or cultivated nursery seeds.

Using a common garden experimental approach, we investigated the extent to which (i) seed provenance and (ii) site of planting, independently or together, influence germination and first-season survival and growth of dominant species in prairie restorations. To investigate these relationships, seeds of three prairie grasses, big bluestem *Andropogon gerardii* Vitman, side-oats grama *Bouteloua curtipendula* (Michx.) Torrey and Indian grass *Sorghastrum nutans* (L.) Nash, were hand-collected from local remnant and restoration sites and purchased from native seed nurseries and then planted as seeds and plugs into three established tallgrass prairie restorations in western Minnesota, USA. We evaluated performance (i.e. germination, survival and growth) of both (iii) transplanted plugs (hereafter plugs) and directly sowed seeds to bridge the conditions experienced by plants in typical restoration practice versus restoration studies [e.g. drilling or broadcasting seed directly into untilled soil with high mortality (Schramm 1990) versus greenhouse or growth chamber studies with generally benign conditions and high survival].

Materials and methods

STUDY SPECIES & SEED SOURCES

Andropogon gerardii, *B. curtipendula* and *S. nutans* are dominant perennial C₄ grasses of the tallgrass prairie (Weaver & Fitzpatrick 1932). These deep-rooted grasses are rhizomatous, polyploid and self-incompatible (De Pisani 2004; Gustafson, Gibson & Nickrent 2004a; Sedivec *et al.* 2009). All have wide geographic distributions and are used extensively in North American prairie restorations (Sedivec *et al.* 2009).

We purchased seed from three Minnesota seed nurseries and hand-collected seed from four remnant and three restoration sites in Douglas County in rural western Minnesota, USA (centred near 45°49' N, 95°43' W; Table 1). Remnants included a virgin prairie preserve, two hillsides and a roadside, each with no history of ploughing (Table 1). Restorations included federal, state and private lands planted within the past 23 years with seed from production fields established from remnant populations within 80 km of the study area (Table 1). We collected seeds between 31st August and 26th September 2009, from up to 50 randomly selected individuals of each species per site (Table 2). Seeds we purchased were grown in production fields located 160–470 km away from Douglas County, which themselves had been established with seeds from prairie remnants 160–550 km away

(Table 1, Appendix S1, Supporting information). Throughout this article, the term 'source type' refers to the remnant, restoration and nursery level, and 'seed source' refers to the ten specific sites from which seeds were collected or purchased. 'Provenance' will refer to both source levels.

We placed hand-collected seed from each plant (hereafter maternal line) into coin envelopes that were stored in freezer bags with silica gel desiccants and transported to the Chicago Botanic Garden. There, envelopes were transferred to paper bags and stored with the nursery seeds in a seed dryer at 14°C and 15% relative humidity. *Andropogon gerardii* and *S. nutans* seeds were cleaned, counted and weighed. We counted and weighed *B. curtipendula* spikelets.

EXPERIMENTAL DESIGN & PREPARATION

We used a common garden design, using both plugs and directly sown seeds, in order to attribute observed phenotypic differences among seeds of different provenances to genetic or environmental causes. To assess the influence that site of planting has on germination and first-season survival and growth, we planted an experimental plot in each of the three source restoration sites.

To quantify the extent to which variation in germination and establishment is linked to provenance for seeds germinated in the

Table 1. *Andropogon gerardii*, *B. curtipendula* and *S. nutans* remnant, restoration and nursery seed source locations and distances (km) to experimental plots located at restoration source sites in rural western Minnesota, USA (original remnant source locations of restoration and nursery seeds are also reported)

	Collection Location				Distance to Experimental Plots (km)			Original Remnant Source Location(s)	
	County, State	Latitude (N)	Longitude (W)	Area (ha)	Rune	Hegg	Mahoney	County, State	Distance (km)
Remnants									
Staffanson Prairie Reserve	Douglas, MN	45°81'05"	95°75'04"	45.0	7.02	7.12	5.37		
JI Case Hill	Douglas, MN	45°85'98"	95°64'19"	2.3	6.47	8.44	4.56		
Hegg Lake East Unit	Douglas, MN	45°76'81"	95°67'38"	5.7	1.88	0.50	4.60		
Hegg Lake NE Corner	Douglas, MN	45°76'69"	95°65'87"	2.5	1.67	0.82	4.60		
Restorations									
Runestone WPA (Federal)	Douglas, MN	45°80'31"	95°65'60"	8.2	–	2.01	3.21	Otter Tail, MN	80
Hegg Lake WMA (State)	Douglas, MN	45°76'64"	95°67'65"	2.4	2.01	–	4.40	Otter Tail, MN	80
								Stevens, MN	45
Mahoney (Private)	Douglas, MN	45°79'94"	95°68'34"	6.0	3.21	4.40	–	Douglas, MN	50
	Production Field Location		Original Remnant Source Location(s)						
	County, State	Distance (km)	<i>A. gerardii</i>		<i>B. curtipendula</i>		<i>S. nutans</i>		
			County, State	Distance (km)	County, State	Distance (km)	County, State	Distance (km)	
Nurseries									
Prairie Restorations, Inc.	Clay, MN	155	Sherburne, MN	160	Sherburne, MN	160	Sherburne, MN	160	
Habitat Forever, LLC	Faribault, MN	320	Polk, MN	250	Houston, MN	470	Kittson, MN	370	
Prairie Moon Nursery, Inc.	Houston, MN	470	Dunn, WI	340	Crawford, WI	550	Green, WI	685	
					Houston, MN	470			

Table 2. Quantities of *A. gerardii*, *B. curtipendula* and *S. nutans* remnant, restoration and nursery seeds collected and germinated in growth chambers (Plugs) or seeded directly into experimental plots (Field)

	<i>A. gerardii</i>					<i>B. curtipendula</i>					<i>S. nutans</i>				
	Maternal Lines		Seeds Used			Maternal Lines		Seeds Used			Maternal Lines		Seeds Used		
	Collected	Used	Plugs	Field	Total	Collected	Used	Plugs	Field	Total	Collected	Used	Plugs	Field	Total
Remnants	179	149	397	697	1094	194	120	1053	2087	3140	200	175	850	4486	5336
Restorations	150	89	544	1530	2074	150	90	781	1536	2317	150	111	898	3811	4709
Nurseries	1.35 kg		810	1800	2610	1.35 kg		810	1800	2610	1.35 kg		810	1800	2610
Total			1751	4027	5778			2644	5423	8067			2558	10 097	12 655

field, we divided seeds from each maternal line into three groups of equal number and placed them in new coin envelopes, each with a randomly assigned row and position in each of three experimental plots (Table 2). We also assigned thirty samples (20 seeds per sample; 5400 in total) from each nursery source to positions and rows in each plot. A total of 19 547 seeds were planted directly in the field (Table 2).

In addition to assessing seeds planted directly in the field, we also investigated the extent to which transplanted seedlings are influenced by provenance and site of planting during early establishment. For this experiment, we selected up to nine seeds from each maternal line, along with 30 samples (nine seeds per sample) from each nursery source, to germinate and grow into plugs in a growth chamber prior to planting them in randomly assigned rows and positions in the same three experimental plots (Table 2). For maternal lines with fewer than 18 seeds, half were chosen at random to be grown into plugs.

We placed seeds in petri dishes lined with blue seed germination blotters (Anchor Paper Company, St. Paul, MN, USA). We placed dishes on trays, which we stored in a growth chamber at 18.3/21.1°C night/day and a light schedule simulating spring day lengths starting with 14 h 20 min of fluorescent light and increasing 2 min 40 s each day. We rotated and watered dishes with distilled water every 48 h. We assessed the germination daily and moved seeds to plugs when the radicle emerged at least 1 mm. Plugs were 2 cm square on top, 4.5 cm deep and filled with Sunshine plug mix (Sun Gro Horticulture, Vancouver, BC, USA). We rotated and watered plug trays from below three times a week and kept them in the same growth chamber. Of the 6953 seeds placed in petri dishes, 3040 sprouted and 1070 survived to be planted in the experimental plots (127 remnant, 370 restoration and 573 nursery).

COMMON GARDEN EXPERIMENT

Between 7th and 9th July, we planted 19 547 seeds and 1070 plugs into three 10 × 10 metre experimental plots located at each of the source restoration sites (Fig. S1, Appendix S1). Seeds and plugs were randomly assigned to rows and positions within plots. At assigned positions, we either planted a plug or poured seeds from a coin envelope in a line along the row and pressed them into the soil. We used toothpicks to mark each planting. Rows were watered once immediately after planting.

Germination (number of seedlings at each position) and growth (height of the longest leaf) of directly sown seedlings

were assessed 1 month after sowing. We recorded survival and growth of directly sown seedlings and plugs 2 months after planting.

We preserved the identities of maternal lines throughout the experiment. All data collection was 'blind' in the sense that measurers identified the seed, seedling or plant by a randomly assigned identifier or location without knowing the source.

STATISTICAL ANALYSIS

We used linear models and generalized linear models (GLMs) to test for effects of provenance, site of planting, seed mass and their interactions on germination, first-season survival and growth of directly sown seeds and plugs of three dominant prairie grasses. We also used a linear model to test whether mean seed mass of maternal lines and nursery samples differed among provenances. Species were evaluated separately. We excluded plants from analyses when their identity was ambiguous, usually due to lost toothpicks. *Andropogon gerardii* plants from J.I. Case Hill were excluded from all analyses due to low seed set. Runestone directly sown seedlings of the same species were excluded from vigour analyses because two or fewer seeds germinated. For all analyses, we used stepwise backwards elimination of non-significant variables ($P \geq 0.05$) to select minimal adequate models (Crawley 2005). Backwards elimination uses sequential likelihood ratio tests to compare models with and without a single focal term.

For directly sown seeds, we analysed the proportion from each maternal line (or nursery sample) that germinated and survived with binomial family GLMs. The residual deviance of the full models greatly exceeded the residual degrees of freedom, indicating overdispersion; therefore, we repeated the analyses assuming a quasibinomial error distribution. To investigate seedling growth 1 and 2 months after planting, we used linear models with mean height of the longest leaf of seedlings at each position as the response variable. Initial explanatory variables included seed source nested within source type (10 sources, except for *A. gerardii*), as well as main and interactive effects of restoration site (three locations), seed source type (remnant, restoration and nursery) and mean seed mass of maternal lines and nursery samples.

For seeds germinated in the growth chamber (i.e. plugs), we used binomial family GLMs to assess the germination and survival at four stages: sprout, when radicles emerged at least 1 mm; plug, when sprouts grew at least one leaf in the plug trays; planting, when plugs were planted in the field; and 2 months, when

Table 3. *Andropogon gerardii*, *B. curtipendula* and *S. nutans* germination and survival at 2 months after planting. Germination shown for seeds grown in a growth chamber and for those directly planted in the field

	Germination		Survival	
	Growth Chamber, %	Field, %	Transplanted Plugs, %	Field, %
<i>A. gerardii</i>	44	7	91	99
<i>B. curtipendula</i>	50	17	87	99
<i>S. nutans</i>	36	3	88	99

plugs had been in the ground for 2 months. The residual deviance of full models did not exceed residual degrees of freedom. Using linear models, we analysed plug growth 2 months after planting with height of the longest leaf as the response. For all plug analyses, initial explanatory variables included source type and seed source nested within source type. We also included

main and interactive effects of plug trays at the plug and planting stages, and restoration site at the 2-month stage.

All analyses were conducted using R (R Core Team 2015). In the event of significant main effects, Tukey's *post hoc* tests were performed using the multcomp package (Hothorn, Bretz & Westfall 2008).

Results

EFFECTS OF PROVENANCE AND RESTORATION SITE ON DIRECTLY SOWN SEEDLINGS

Germination of seeds in the field was low; however, post-germination survival exceeded 99% for all three species (Table 3). Neither provenances nor restoration sites were consistent predictors of germination and survival among species. Germination and survival of *A. gerardii* and *B. curtipendula* differed among sites, among source types

Table 4. Likelihood ratio tests for stepwise model simplification using backwards elimination for analyses of *A. gerardii*, *B. curtipendula* and *S. nutans* directly sown seedling germination (a), survival until 2 months after planting (b) and vigour (mean longest leaf height of seedlings from each maternal line) one (c) and 2 months after planting (d)

Focal term (interaction or factor)	<i>A. gerardii</i>			<i>B. curtipendula</i>			<i>S. nutans</i>		
	d.f.	Deviance	<i>P</i>	d.f.	Deviance	<i>P</i>	d.f.	Deviance	<i>P</i>
(a) Germination									
source [source type]	6	31.7	0.02	7	114.0	< 0.0001	7	20.5	0.21
source type × seed mass	2	8.7	0.13	2	12.4	0.05	2	1.4	0.73
site × seed mass	2	4.4	0.36	2	6.4	0.21	2	23.6	0.005
site × source type	4	14.7	0.15	4	6.5	0.53	4	30.6	0.008
seed mass	1	0.01	0.96	1	7.4	0.06	1	4.5	0.16
source type	2	46.5	< 0.0001	2	37.3	0.0002	2	2.2	0.63
site	2	33.9	0.0004	2	120.4	< 0.0001	2	46.4	< 0.0001
(b) Survival (2 months)									
source [source type]	6	36.5	0.004	7	110.0	< 0.0001	7	11.9	0.67
source type × seed mass	2	14.6	0.02	2	6.2	0.22	2	0.03	0.99
site × seed mass	2	6.7	0.17	2	10.5	0.08	2	15.5	0.04
site × source type	4	15.8	0.08	4	3.8	0.77	4	24.0	0.04
seed mass	1	0.4	0.68	1	26.0	0.0006	1	0.1	0.88
source type	2	43.0	< 0.0001	2	120.0	< 0.0001	2	0.2	0.97
site	2	46.1	< 0.0001	2	113.4	< 0.0001	2	85.7	< 0.0001
Focal term (interaction or factor)	d.f.	Sum of sq	<i>P</i>	d.f.	Sum of sq	<i>P</i>	d.f.	Sum of sq	<i>P</i>
(c) Vigour (1 month)									
source [source type]	5	3670.0	0.23	7	1667.4	0.55	7	12 928.0	0.02
source type × seed mass	2	373.1	0.71	2	512.9	0.40	2	1973.2	0.28
site × seed mass	2	1103.8	0.36	2	964.2	0.18	2	103.7	0.93
site × source type	4	952.4	0.77	4	1236.4	0.36	4	950.1	0.87
seed mass	1	894.0	0.19	1	865.6	0.08	1	2637.9	0.06
source type	2	86.4	0.92	2	4599.9	0.0004	2	4009.0	0.08
site	2	2374.1	0.11	2	2735.5	0.009	2	1553.2	0.36
(d) Vigour (2 months)									
source [source type]	5	1726.1	0.70	7	3050.4	0.41	7	13 672.0	0.13
source type × seed mass	2	2869.3	0.08	2	855.7	0.37	2	135.5	0.95
site × seed mass	2	879.4	0.47	2	307.4	0.70	2	2335.8	0.38
site × source type	4	862.8	0.82	4	2979.4	0.14	4	1313.8	0.90
seed mass	1	102.0	0.67	1	1443.4	0.07	1	1509.5	0.26
source type	2	3625.4	0.04	2	5974.1	0.001	2	3739.6	0.21
site	2	435.5	0.68	2	2227.7	0.08	2	6223.2	0.08

Values significant at the $P \leq 0.05$ are in bold

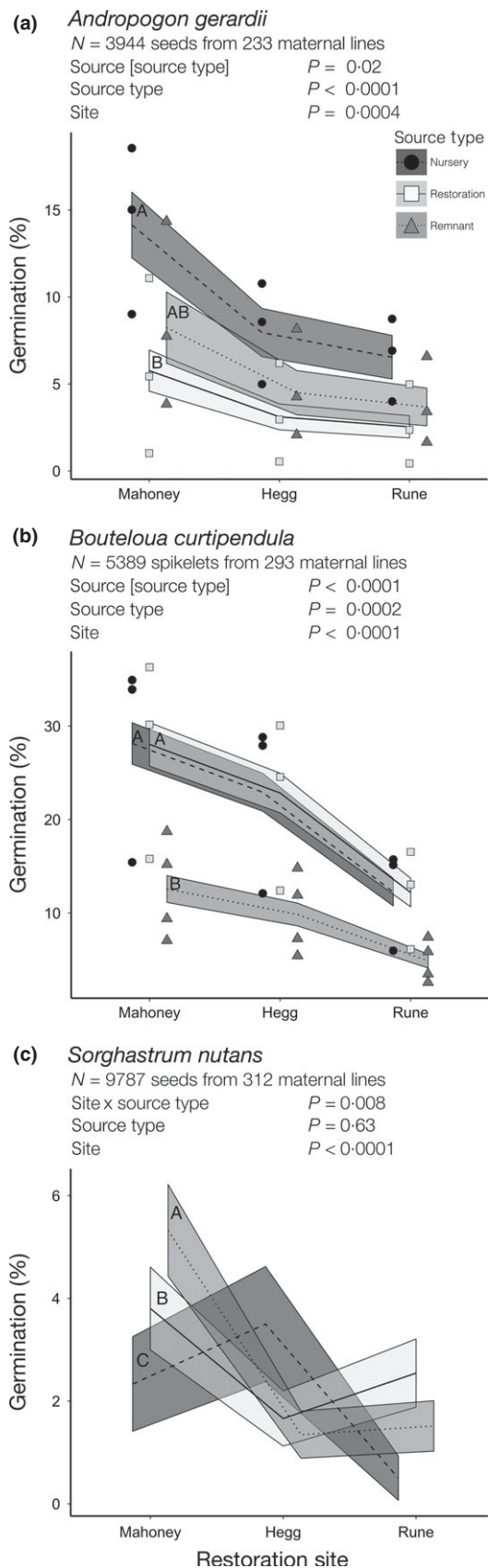


Fig. 1. Germination of *A. gerardii*, *B. curtipendula* and *S. nutans* directly sown seedlings, assessed 1 month after planting into three experimental plots. Estimates based on minimal adequate generalized linear models with quasibinomial response. Points show mean values for each seed source \times site combination. Shaded areas represent standard error (SE) for each source type. For each source type, means with the same letter were not significantly different based on Tukey's HSD pairwise comparisons ($P < 0.05$). Letters in panel (c) indicate the significant interaction term.

and among seed sources nested within source types, and these effects were additive (Table 4). In contrast, the influence of source type on *S. nutans* germination and survival varied among restoration sites (Table 4), with the germination of nursery seeds showing an opposite trend compared to the other source types (Fig. 1c).

With the exception of *S. nutans* nursery seeds, germination was consistently higher at the Mahoney site than at other restoration sites among all species (Fig. 1). There were, however, few consistent patterns among species in the ranking of source types. *Andropogon gerardii* nursery seeds had significantly higher germination than restoration seeds, but not remnant seeds, which were intermediate to the other source types (Fig. 1a). Germination of *B. curtipendula* nursery and restoration seeds did not differ significantly from each other, but both had significantly higher germination than remnant seeds (Fig. 1b). For *S. nutans* germination, however, the ranking of source types differed among sites, with each of the three seed source types outperforming the rest at different sites (Fig. 1c).

Nested within source types, there were significant differences in germination and survival among seed sources for both *A. gerardii* and *B. curtipendula* seeds (Table 4). Germination of two *A. gerardii* nursery sources was between 3–5% higher than that of the third source (Tukey's HSD, $P < 0.05$, Fig. 1a). Two each of the *B. curtipendula* nursery and restoration seed sources had germination that was more than double that of the remaining sources (Tukey's HSD, $P < 0.05$, Fig. 1b).

The influences of provenance and restoration site on first-season growth of directly sown seedlings varied among species (Table 4). Seed source type influenced *A. gerardii* and *B. curtipendula* vigour 2 months after planting (Table 4), such that nursery seedlings were consistently taller than seedlings of other source types (Fig. 2a,b). Nested within source types, there were significant differences in *S. nutans* seedling growth among the seed sources during the first month, but this pattern disappeared by the second month (Table 4, Fig. 2c). *Bouteloua curtipendula* seedling vigour differed among sites 1 month after planting (Table 4), with seedlings that were generally taller at Mahoney than at Runestone, but this

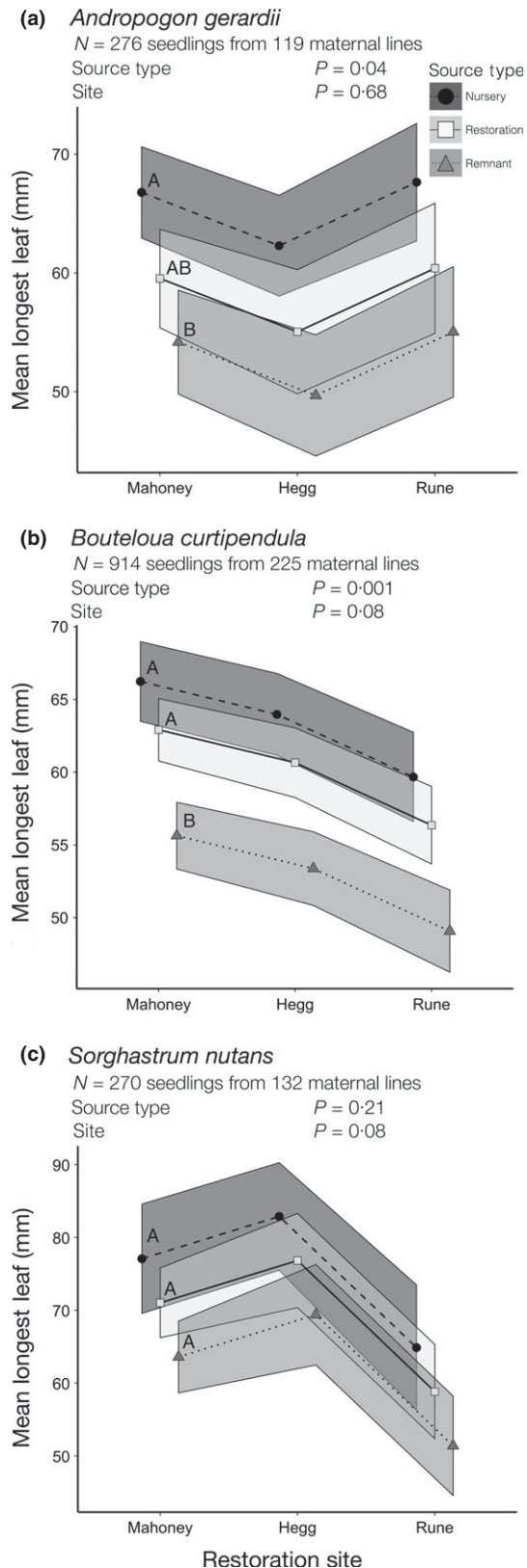


Fig. 2. Mean longest leaf of *A. gerardii*, *B. curtipendula* and *S. nutans* directly sown seedlings from each maternal line (or nursery sample), assessed 2 months after planting. Estimates based on minimal adequate linear models. Shaded areas represent SE for each source type, and those with the same letter were not significantly different ($P < 0.05$).

trend became non-significant later in the season (Fig 2b). *Sorghastrum nutans* seedlings were also shorter at Runestone, but this pattern was similarly non-significant (Table 4). Seeds from restoration sites did not exhibit home-site advantages in germination, survival or vigour, except where differences were negligible in one case (data not shown).

Seed mass differed among provenances in most cases; however, the rankings among source types and among sources nested within source types varied among species (Fig. 3). In all species, seeds from remnant sources had the lowest mass and restoration seed masses varied among the three restoration sources (Fig. 3). The impact of seed mass on germination was inconsistent among species. Seed mass effects on *B. curtipendula* germination differed among source types (Table 4), with a positive relationship for remnant and restoration seeds, but a negative relationship in nursery seeds (Fig. 4a). In contrast, the influence of seed mass on *S. nutans* germination varied among restoration sites (Table 4). Germination increased with seed mass at Runestone, but decreased at the other two restoration sites (Fig. 4b). We found no evidence of seed mass effects on growth or on *A. gerardii* seedlings at all (Table 4).

EFFECTS OF PROVENANCE AND RESTORATION SITE ON PLUGS

Seed germination was 3–12 times higher in the growth chambers than in the field (Table 3). While survival between germination in the growth chambers and planting in the field was low (*A. gerardii* 32%, *B. curtipendula* 58% and *S. nutans* 21%), after planting, plug survival was higher (Table 3). Overall, germination and survival were 3–6 times higher for transplants than for directly sown seeds (Table 3).

Seed source type influenced germination and survival of plugs at all four of the growth stages (sprout, plug, planting and 2 months) for all species (Table 5). Nested within source type, germination and survival at the plug and planting stages differed among the seed sources for all species, and at the 2-month stage for *S. nutans* (Table 5). Neither tray nor restoration site influenced plug survival in any species (Table 5).

Mean survival of *A. gerardii* nursery plugs was higher than that of both restoration and remnant plugs (Fig. 5a). *Bouteloua curtipendula* germination of nursery and restoration plugs exceeded remnant plugs by more than 30% (Fig. 5b). In contrast, germination of *S. nutans* from nursery sources was 33% lower than that of plugs from restoration sources and 16% lower than that of remnant sources (Fig. 5c).

Plug growth 2 months after planting differed among restoration sites for all species (Tukey's HSD, $P < 0.05$), while provenance influenced only *S. nutans* and *B. curtipendula* growth (Table 5). All plugs, regardless of source type or species, were tallest at the Mahoney site, and most

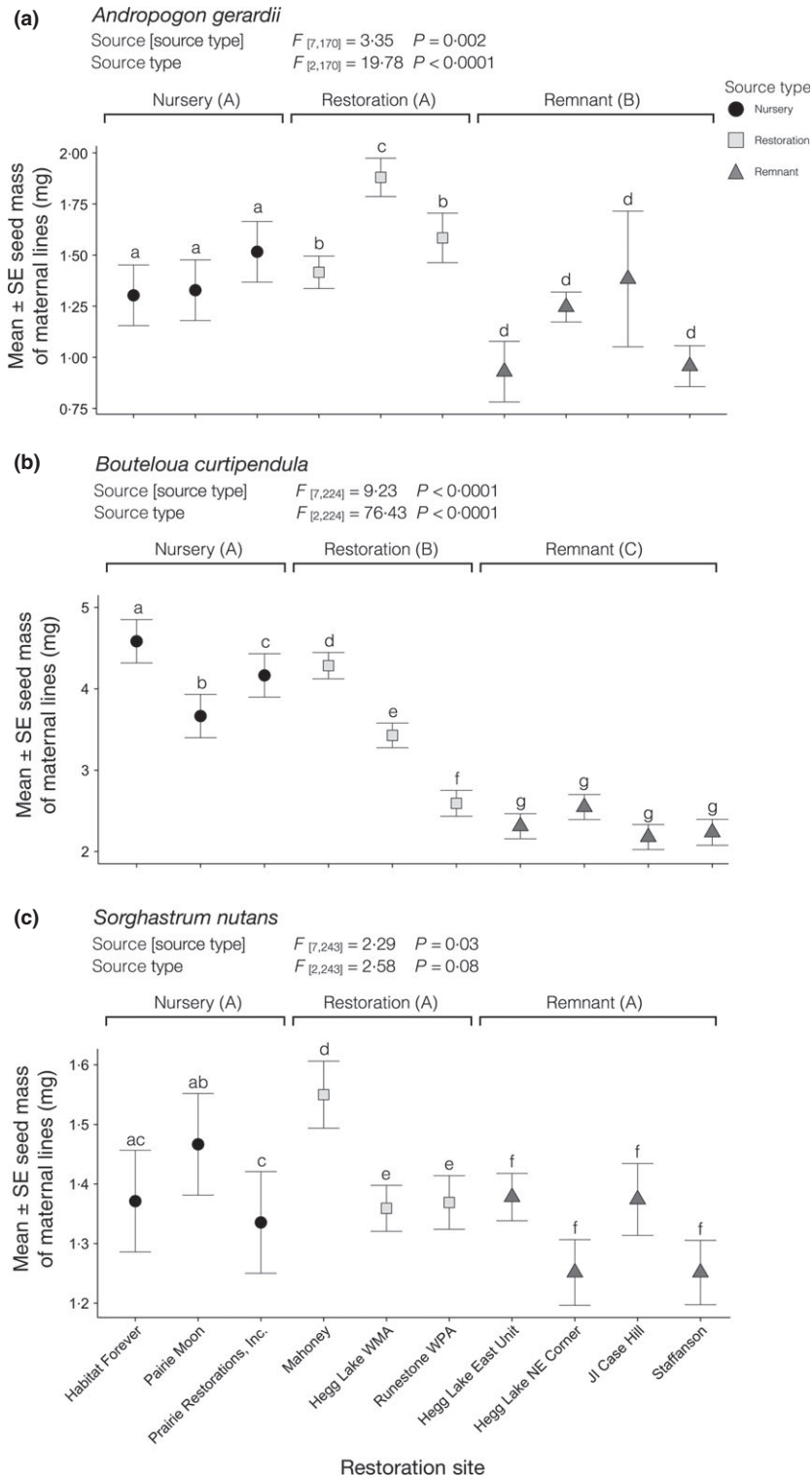


Fig. 3. Seed mass of *A. gerardii*, *B. curtipendula* and *S. nutans* maternal lines. Estimates based on minimal adequate linear models. Source types (uppercase) and sources nested within source types (lowercase) with the same letter were significantly different ($P < 0.05$).

were shortest at Runestone (Table S2, Appendix S2). Seed source type influenced *B. curtipendula* vigour (Table 5), such that nursery seedlings were consistently taller than seedlings of other source types (Table S2, Appendix S2). Nested within source types, *S. nutans* and *B. curtipendula* seedling growth differed significantly among seed sources (Table 5).

Discussion

Little consensus exists about the relative importance of seed provenance, site characteristics and planting methods in prairie restorations. Our results confirm these general findings for dominant warm-season grasses: effects of provenance and restoration site were species specific, and summer

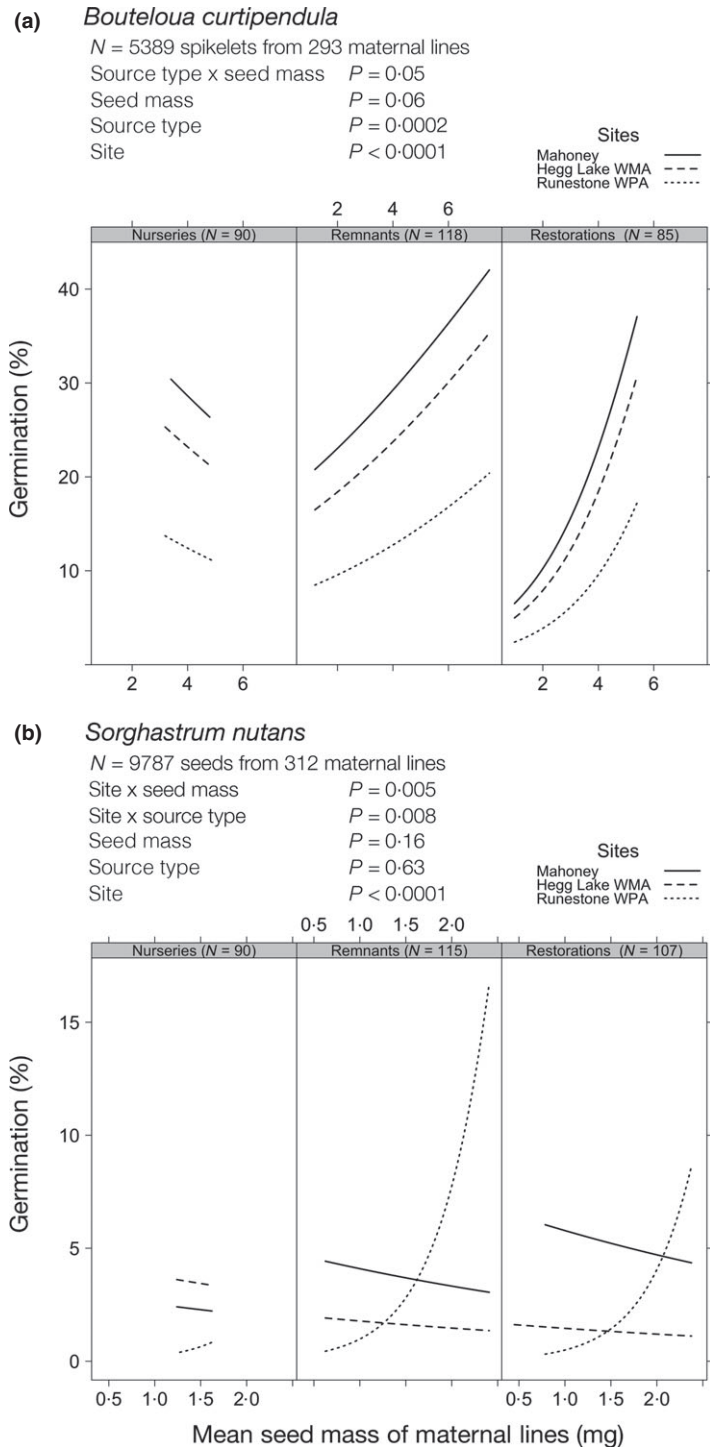


Fig. 4. Germination rates of dominant prairie grasses (a) *B. curtipendula* and (b) *S. nutans* predicted from seed mass of three source types planted at three restoration sites. Seed mass was estimated as mean spikelet or seed mass from each maternal line or from thirty samples (20 seeds per sample) from nursery spikelets or seeds. Prediction lines are shown over the range of masses present and result from the best-fit generalized linear model for each species.

seed germination in the field was a limiting step in restoration success. Moreover, we found little evidence for local adaptation in germination or first-season survival and growth.

EFFECTS OF PROVENANCE

Seed provenance influenced germination, survival and growth in *A. gerardii*, *S. nutans* and *B. curtipendula*, with the exception of directly sown *S. nutans* and vigour of plug-grown *A. gerardii*. The strength of provenance effects

differed among species and between planting plugs versus directly sown seeds. When provenance effects were significant, performance was usually similar among sources of the same type and, despite expectations (Wilkinson 2001; McKay *et al.* 2005), generally highest among non-local nursery sources and lowest among local remnant sources. We discuss three mechanisms that may contribute to provenance effects on plant performance.

First, genetic differences resulting from selection may contribute to the (generally) superior performance of

Table 5. Likelihood ratio tests for stepwise model simplification using backwards elimination for analyses of *A. gerardii*, *B. curtipendula* and *S. nutans* plug germination and survival at four stages: sprout, when the radicle emerged at least 1 mm (a); plug, when sprouts grew at least one leaf in the plug trays (b); planting, when plugs were planted in the field (c); and 2 months, when plugs had been in the ground for 2 months (d). Plug growth (height of the longest leaf) 2 months after plantings also included (e)

Focal term (interaction or factor)	<i>A. gerardii</i>			<i>B. curtipendula</i>			<i>S. nutans</i>		
	d.f.	Deviance	<i>P</i>	d.f.	Deviance	<i>P</i>	d.f.	Deviance	<i>P</i>
(a) Germination (sprout)									
source [source type]	6	1063.8	<0.0001	7	1063.8	<0.0001	7	790.9	<0.0001
source type	2	189.6	<0.0001	2	189.6	<0.0001	2	1129.6	<0.0001
(b) Survival (plug)									
source [source type]	6	102.3	<0.0001	7	80.0	<0.0001	7	66.6	<0.0001
tray × source type	16	4.3	1.00	33	33.3	0.45	34	37.1	0.33
source type	2	641.5	<0.0001	2	1812.3	<0.0001	2	39.5	<0.0001
tray	8	1.7	0.99	17	11.5	0.83	17	26.5	0.07
(c) Survival (planting)									
source [source type]	6	24.5	0.0004	7	37.3	<0.0001	7	252.2	<0.0001
tray × source type	16	1.8	1.00	32	20.5	0.94	34	33.0	0.52
source type	2	99.2	<0.0001	2	427.4	<0.0001	2	163.4	<0.0001
tray	8	3.0	0.93	17	6.2	0.99	17	19.5	0.30
(d) Survival (2 months)									
source [source type]	6	3.7	0.71	7	5.7	0.57	1	126.7	<0.0001
site × source type	4	0.6	0.96	4	2.9	0.57	4	0.4	0.98
source type	2	39.6	<0.0001	2	95.8	<0.0001	2	31.2	<0.0001
site	2	2.8	0.27	2	2.6	0.27	2	1.7	0.43
Focal term (interaction or factor)	d.f.	Sum of sq	<i>P</i>	d.f.	Sum of sq	<i>P</i>	d.f.	Sum of sq	<i>P</i>
(e) Vigour (2 months)									
source [source type]	6	260.6	0.14	7	1683.1	<0.0001	7	1525.4	<0.0001
site × source type	4	28.8	0.90	4	32.9	0.92	4	79.5	0.50
source type	2	14.1	0.77	2	178.0	0.09	2	1259.7	<0.0001
site	2	8174.8	<0.0001	2	15 410.0	<0.0001	2	5753.2	<0.0001

Values significant at $P \leq 0.05$ are in bold

A. gerardii and *B. curtipendula* nursery and restoration seedlings. Plants in production fields and restorations experience different selective pressures than their counterparts in remnants. In remnants, seedlings compete with other plants for light, nutrients and water (Weaver & Fitzpatrick 1932), whereas in production fields and restorations, mowing, herbicides and controlled burns reduce competition (Schramm 1990). Under managed conditions, shifts in genotypic frequency and life-history traits may occur quickly (Vander Mijnsbrugge, Bischoff & Smith 2010; Aavik *et al.* 2012; Schröder & Prasse 2013), resulting in seeds adapted to conditions present during restoration establishment. In this study, we used pre-existing restorations but cleared above-ground vegetation. In these conditions, mean germination of *B. curtipendula* seed from nursery and restoration sources was more than twice that of remnants, providing evidence that they are suited to establishment in restoration conditions.

Secondly, some of the variation in performance among seed provenances may be due to non-genetic effects resulting from differences in parental environment. Resource availability to parents often correlates with seed mass and

germination (Roach & Wulff 1987; Galloway 2005). If this were the case here, we would expect parental provisioning (i.e. seed mass) to positively correlate with seedling germination. Seed mass influenced *B. curtipendula* and *S. nutans* germination, but the relationship was not consistently positive among source types, in the case of *B. curtipendula*, or sites, in the case of *S. nutans*. The relationship between parental environment, seed mass and germination often depends in part on offspring environment, making it difficult to separate genetic and environmental parental effects in a single generation (Bischoff *et al.* 2006). Nevertheless, our results suggest that, for some prairie grasses, the parental environment influences progeny success.

Thirdly, seeds sourced from remnants may experience lower first-season performance resulting from genetic issues unrelated to local adaptation, including genetic drift and inbreeding (Hufford & Mazer 2003). These genetic processes are expected in small and isolated populations, including prairie remnants. Many studies have shown a substantial variation in genetic diversity and in plant performance among small populations (Gustafson, Gibson & Nickrent 2004a; Moncada *et al.* 2007; Dolan, Marr &

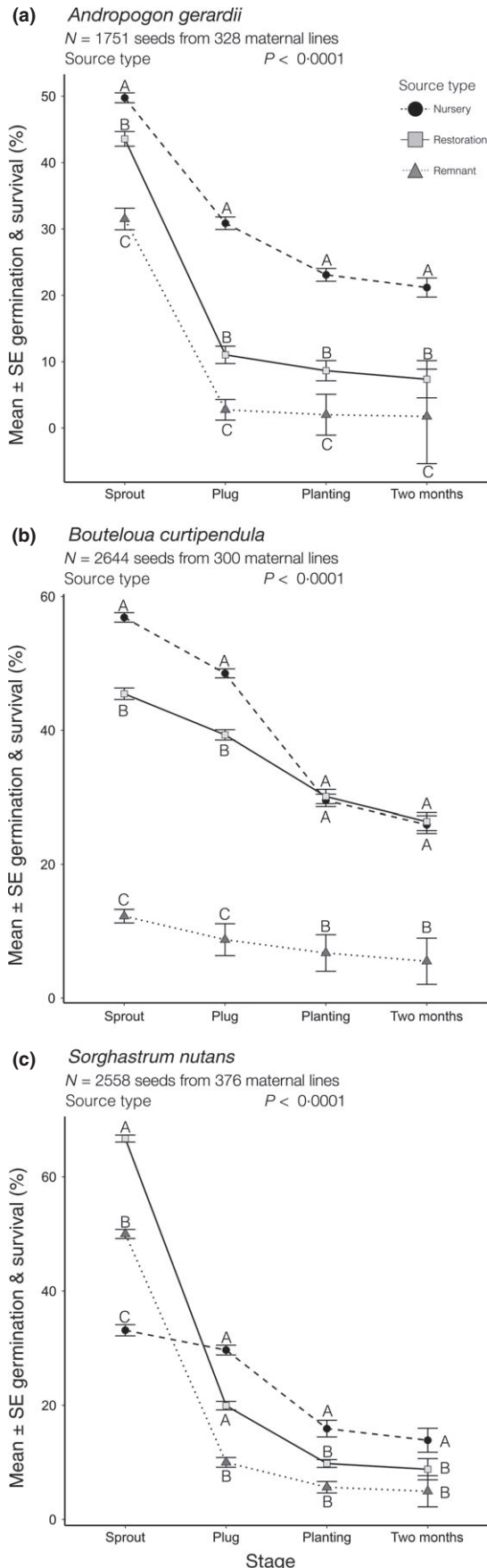


Fig. 5. *Andropogon gerardii*, *B. curtipendula* and *S. nutans* plug germination and survival at four growth stages (sprout, plug, planting and 2 months). Estimates based on one generalized linear models with binomial response for each stage. Means with the same letter were not significantly different ($P < 0.05$).

Schnabel 2008; Seifert & Fischer 2010). It is important to note, however, that low fitness due to non-random mating, inbreeding depression, would disappear in a generation with random mating among plants from multiple sources. Our results are consistent with expectations of plant performance in the seeds sampled from small remnant populations. Common garden studies alone cannot detect whether morphological differences are due to adaptation, parental effects or inbreeding (Kramer & Havens 2009).

Germination and first-season survival and growth are crucial for restoration success, and we should limit our inference from this study to these early life-history traits. For example, using seeds generated by crossing genotypes from multiple, formerly isolated, remnant populations in production fields may result in outbreeding depression when plants start reproducing, which may be detrimental in the long term (Hufford & Mazer 2003; Kramer & Havens 2009). Similarly, the existence of multiple ploidy races within dominant grass species may undermine restoration efforts in the long term. Ploidy races may have substantial mating incompatibilities and also differ in mycorrhizal associations and competitive abilities, increasing the importance of using appropriate genetic sources (Gustafson, Gibson & Nickrent 2004a; Rogers & Montalvo 2004). Additionally, plant diversity in restorations often decreases as productivity of dominant grasses increases (Baer *et al.* 2004; Wilsey 2010; Lambert, Baer & Gibson 2011; Gibson *et al.* 2013; Grman, Bassett & Brudvig 2013). Therefore, the inclusion of non-local seeds with enhanced competitive physiologies may reduce species diversity. It is also important to note that long-term consequences of seed selection decisions for restoration success may be influenced by traits that are not evident in the first season, such as variation in growth form, phenology and competitive ability, and there may be important trade-offs between early establishment of larger seeds from less fragmented sources versus traits that influence later survival and reproduction (Gustafson, Gibson & Nickrent 2004b, 2005; Klopff & Baer 2011; Schröder & Prasse 2013).

EFFECTS OF RESTORATION SITE

The C_4 species studied here differed in their responses to environmental variation when seeded directly in the field. Whereas *Andropogon gerardii* vigour did not vary among restoration sites, *B. curtipendula* seedlings were sensitive to environmental variation, particularly during the first month. Moreover, while site influenced the germination for all species, the effects of both source type and seed mass on *S. nutans* germination varied among sites, as evidenced by significant interaction terms in statistical mod-

els. These findings are consistent with other studies that have found important differences among dominant grass species in their physiological performance, competitive ability, dominance and response to altered resource conditions such as reduced nitrogen and water availability (Silletti & Knapp 2001; Wilsey 2010; Klopff & Baer 2011; Lambert, Baer & Gibson 2011; Grman, Bassett & Brudvig 2013). The existence of such important differences among 'ecologically similar' species suggests that practitioners should be cautious when generalizing about restoration practices from studies of 'similar' grass species in prairie ecosystems.

EFFECTS OF PLANTING METHOD

Planting method strongly influenced germination, first-season survival and growth for all species. Germination was 3–12 times higher in the growth chambers than in the field, and overall plug survival was 3–6 greater than that of directly sown seedlings. These differences may result from challenging field conditions, including intermittent rainfall, competition with existing vegetation and mid-summer planting. Timing of planting and assembly history may impact short- and long-term outcomes in tallgrass prairie restorations, with better outcomes when seeding natives in the spring (Martin & Wilsey 2012, 2014). Nevertheless, our results reinforce the conclusion that germination is a critical stage in restoration establishment (Middleton, Bever & Schultz 2010; Seifert & Fischer 2010). Using plugs, however, is often logistically and economically unrealistic. Restorations using directly sown seeds may improve outcomes by adding seeds multiple times (Middleton, Bever & Schultz 2010), but such additions may not shift an established community from an exotic to native state (Martin & Wilsey 2014). Seed mixes are, therefore, likely a critical factor in determining restoration outcomes (Wilsey 2010; Grman, Bassett & Brudvig 2013). Early establishment of natives can inhibit exotic invasion, but overdominance of native grasses can suppress native diversity (Seifert & Fischer 2010; Wilsey 2010; Stevens & Fehmi 2011; Martin & Wilsey 2012; Grman, Bassett & Brudvig 2013). However, Middleton, Bever & Schultz (2010) found that supplemental use of plugs during the first 4 years of restoration resulted in greater species richness and diversity. Managers should consider supplementing seeded restorations with plugs to increase native diversity.

SYNTHESIS AND APPLICATIONS

Both seed provenance and site characteristics affected dominant warm-season grass performance during the first season, but the importance of these factors differed substantially among species. *Sorghastrum nutans* and *B. curtipendula* were particularly sensitive to environmental conditions at the restoration sites, while provenance greatly influenced *A. gerardii* and *B. curtipendula* performance. It is clear that environmental factors influencing

performance may vary among seemingly similar sites over relatively small spatial scales (Bakker *et al.* 2003). Our study was not designed to distinguish which aspects of the environment contributed to these differences. Management decisions about seed mix composition, diversity and density have considerable influence on restoration outcomes (Grman, Bassett & Brudvig 2013), and land managers should consider each species separately, particularly among dominant species. Variation in performance among seed provenances for *A. gerardii* and *B. curtipendula* may have important consequences for diversity and function of restored ecosystems.

Seeds propagated in fields, either from local sources, such as restorations, or from distant nurseries, generally had enhanced germination, survival and vigour compared to seeds collected from local remnants. If productivity is a priority, then propagated sources may be desirable; however, if species diversity is a priority, then collecting seeds of certain dominant species from local remnants may be worthwhile. Furthermore, the use of local sources diminishes the risk of spreading undesired genotypes (Bischoff, Steinger & Müller-Schärer 2010). We quantified strong effects of source in establishment, but other studies are needed to assess long-term effects on restoration outcomes and to identify the basis for variation in performance among provenances (e.g. adaptation, genetic drift or parental effects).

Acknowledgments

We thank Chad Raitz (US Fish and Wildlife Service), Kevin Kotts (Minnesota DNR), Robert Mahoney, The Nature Conservancy and anonymous landowners for permission to work on their land. Team Echinacea (2009 and 2010) and the Chicago Botanic Garden community, including over 20 volunteers, family members and interns helped with field and laboratory work. Krissa Skogen, Joe Walsh, Diane Campbell and anonymous reviewers provided helpful feedback. The Garden Club of America, the Harris Family Foundation and NSF (0545072) supported this work.

Data accessibility

Data available from the Dryad Digital Repository doi:10.5061/dryad.r7g8q (Gallagher & Wagenius 2015).

References

- Aavik, T., Edwards, P.J., Holderegger, R., Graf, R. & Billeter, R. (2012) Genetic consequences of using seed mixtures in restoration: a case study of a wetland plant *Lychnis flos-cuculi*. *Biological Conservation*, **145**, 195–204.
- Baer, S.G., Blair, J.M., Collins, S.L. & Knapp, A.K. (2004) Plant community responses to resource availability and heterogeneity during restoration. *Oecologia*, **139**, 617–629.
- Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G. & Waddington, J. (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, **13**, 137–153.
- Basey, A.C., Fant, J.B. & Kramer, A.T. (2015) Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. *Native Plants Journal*, **16**, 37–53.
- Bischoff, A., Steinger, T. & Müller-Schärer, H. (2010) The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. *Restoration Ecology*, **18**, 338–348.

- Bischoff, A., Vonlanthen, B., Steinger, T. & Müller-Schärer, H. (2006) Seed provenance matters – effects on germination of four plant species used for ecological restoration. *Basic and Applied Ecology*, **7**, 347–359.
- Clausen, J., Keck, D.D. & Heisey, W.M. (1941) Regional differentiation in plant species. *American Naturalist*, **75**, 231–250.
- Crawley, M.J. (2005) *Statistics: An Introduction Using R*. John Wiley & Sons Ltd, Chichester.
- De Pisani, M.A.L.T. (2004) *Ecological implications of genetic variation in Bouteloua curtipendula (Michx.) Torr.* PhD thesis, Texas A&M University.
- Dolan, R.W., Marr, D.L. & Schnabel, A. (2008) Capturing genetic variation during ecological restorations: an example from Kankakee Sands in Indiana. *Restoration Ecology*, **16**, 386–396.
- Etterson, J.R. & Shaw, R.G. (2001) Constraint to adaptive evolution in response to global warming. *Science*, **294**, 151–154.
- Frankel, O.H. & Soule, M.E. (1981) *Conservation and Evolution*. Cambridge University Press, Cambridge.
- Gallagher, M.K. & Wagenius, S.W. (2015) Data from: seed source impacts germination and early establishment of dominant grasses in prairie restorations. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.r7g8q>.
- Galloway, L.F. (2005) Maternal effects provide phenotypic adaptation to local environmental conditions. *New Phytologist*, **166**, 93–100.
- Gibson, D.J., Baer, S.G., Klopff, R.P., Reed, L.K., Wodika, B.R. & Willand, J.E. (2013) Limited effects of dominant species population source on community composition during community assembly. *Journal of Vegetation Science*, **24**, 429–440.
- Grman, E., Bassett, T. & Brudvig, L.A. (2013) EDITOR'S CHOICE: confronting contingency in restoration: management and site history determine outcomes of assembling prairies, but site characteristics and landscape context have little effect. *Journal of Applied Ecology*, **50**, 1234–1243.
- Gustafson, D.J., Gibson, D.J. & Nickrent, D.L. (2004a) Conservation genetics of two co-dominant grass species in an endangered grassland ecosystem. *Journal of Applied Ecology*, **41**, 389–397.
- Gustafson, D.J., Gibson, D.J. & Nickrent, D.L. (2004b) Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. *Functional Ecology*, **18**, 451–457.
- Gustafson, D.J., Gibson, D.J. & Nickrent, D.L. (2005) Using local seeds in prairie restoration: data support the paradigm. *Native Plants Journal*, **6**, 25–28.
- Hereford, J. (2009) A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist*, **173**, 579–588.
- Hoekstra, J.M., Boucher, T.M., Ricketts, T.H. & Roberts, C. (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29.
- Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.
- Hufford, K.M. & Mazer, S.J. (2003) Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution*, **18**, 147–155.
- Johnson, R., Stritch, L., Olwell, P., Lambert, S., Horning, M.E. & Cronn, R. (2010) What are the best seed sources for ecosystem restoration on BLM and USFS lands? *Native Plants Journal*, **11**, 117–131.
- Klopff, R.P. & Baer, S.G. (2011) Root dynamics of cultivar and non-cultivar population sources of two dominant grasses during initial establishment of tallgrass prairie. *Restoration Ecology*, **19**, 112–117.
- Kramer, A.T. & Havens, K. (2009) Plant conservation genetics in a changing world. *Trends in Plant Science*, **14**, 599–607.
- Lambert, A.M., Baer, S.G. & Gibson, D.J. (2011) Intraspecific variation in ecophysiology of three dominant prairie grasses used in restoration: cultivar versus non-cultivar population sources. *Restoration Ecology*, **19**, 43–52.
- Lesica, P. & Allendorf, F.W. (1999) Ecological genetics and the restoration of plant communities: mix or match. *Restoration Ecology*, **7**, 42–50.
- Martin, L.M. & Wilsey, B.J. (2012) Assembly history alters alpha and beta diversity, exotic-native proportions and functioning of restored prairie plant communities. *Journal of Applied Ecology*, **49**, 1436–1445.
- Martin, L.M. & Wilsey, B.J. (2014) Native-species seed additions do not shift restored prairie plant communities from exotic to native states. *Basic and Applied Ecology*, **15**, 297–304.
- McKay, J.K., Christian, C.E., Harrison, S. & Rice, K.J. (2005) “How local is local?” – A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology*, **13**, 432–440.
- Middleton, E.L., Bever, J.D. & Schultz, P.A. (2010) The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. *Restoration Ecology*, **18**, 181–187.
- Moncada, K.M., Ehlke, N.J., Muehlbauer, G.J., Sheaffer, C.C., Wyse, D.L. & Dehaan, L.R. (2007) Genetic variation in three native plant species across the state of Minnesota. *Crop Science*, **47**, 2379–2389.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Reed, D.H. & Frankham, R. (2003) Correlation between fitness and genetic diversity. *Conservation Biology*, **17**, 230–237.
- Roach, D.A. & Wulff, R.D. (1987) Maternal effects in plants. *Annual Review of Ecology and Systematics*, **18**, 209–235.
- Rogers, D.L. & Montalvo, A.M. (2004) Genetically appropriate choices for plant materials to maintain biological diversity. University of California, Report to the USDA Forest Service, Rocky Mountain Region, Lakewood, CO. Online: <http://www.fs.fed.us/r2/publications/botany/plantgenetics.pdf>
- Sackville Hamilton, N.R. (2001) Is local provenance important in habitat creation? A reply. *Journal of Applied Ecology*, **38**, 1374–1376.
- Samson, F. & Knopf, F. (1994) Prairie conservation in North America. *BioScience*, **44**, 418–421.
- Schramm, P. (1990) Prairie restoration: a twenty-five year perspective on establishment and management. *Proceedings of the 12th North American Prairie Conference* (eds D.D. Smith & C.A. Jacobs), pp. 169–178. University of Northern Iowa, Cedar Rapids, IA.
- Schröder, R. & Prasse, R. (2013) Cultivation and hybridization alter the germination behavior of native plants used in revegetation and restoration. *Restoration Ecology*, **21**, 793–800.
- Sedivec, K.K., Tober, D.A., Duckwitz, W.L., Dewald, D.D., Printz, J.L. & Craig, D.J. (2009) *Grasses for the Northern Plains: Growth Patterns, Forage Characteristics and Wildlife Values. Volume II - Warm-Season Grasses*. USDA NRCS & NDSU Extension Service, Fargo, North Dakota.
- Seifert, B. & Fischer, M. (2010) Experimental establishment of a declining dry-grassland flagship species in relation to seed origin and target environment. *Biological Conservation*, **143**, 1202–1211.
- Sillett, A.M. & Knapp, A.K. (2001) Responses of the codominant grassland species *Andropogon gerardii* and *Sorghastrum nutans* to long-term manipulations of nitrogen and water. *American Midland Naturalist*, **145**, 159–167.
- Stevens, J.M. & Fehmi, J.S. (2011) Early establishment of a native grass reduces the competitive effect of a non-native grass. *Restoration Ecology*, **19**, 399–406.
- Vander Mijnsbrugge, K., Bischoff, A. & Smith, B. (2010) A question of origin: where and how to collect seed for ecological restoration. *Basic and Applied Ecology*, **11**, 300–311.
- Weaver, J.E. & Fitzpatrick, T.J. (1932) Ecology and relative importance of the dominants of tall-grass prairie. *Botanical Gazette*, **93**, 113–150.
- Wilkinson, D.M. (2001) Is local provenance important in habitat creation? *Journal of Applied Ecology*, **38**, 1371–1373.
- Wilsey, B.J. (2010) Productivity and subordinate species response to dominant grass species and seed source during restoration. *Restoration Ecology*, **18**, 628–637.

Received 16 June 2015; accepted 23 October 2015
 Handling Editor: Brian Wilsey

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Sampling scheme and provenance history.

Appendix S2. Plug leaf height.