

RESEARCH ARTICLE

# Persistence of native and exotic plants 10 years after prairie reconstruction

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Prairie reconstructions are a critical component of preservation of the imperiled tallgrass prairie ecosystem in the Midwestern United States. Sustainability of this endeavor depends on establishment of persistent cover of planted native species and resistance to noxious weeds. The goal of this study was to understand the influence of early reconstruction practices on long-term outcomes. Twelve replicates of three planting methods (dormant-season broadcast, growing-season broadcast, and growing-season drill) and three seed mix richness levels (10, 20, or 34 species), fully crossed in a completely randomized design were planted in 2005 on nine former agricultural fields located in Iowa and Minnesota. Cover by species was estimated in 2005–2007, 2010, and 2015. In 2015, cover of planted species, native nonplanted species, and exotic species were similar to those recorded in 2010. Cover of the noxious weed *Cirsium arvense* had also declined by an average of 49% without herbicide from a peak in 2007 to low stable levels from 2010 to 2015. Richness of planted forbs, on the other hand, were still increasing in high-richness broadcast treatments (e.g. 17–59% increase 2010–2015 in Minnesota). Two results in 2015 are reasons for concern: cover of planted species is only slightly over 50% in both Minnesota and Iowa, though with forbs still increasing, this may improve; and the cool-season exotic grasses *Poa pratensis* and *Bromus inermis* are increasing at both Minnesota and Iowa sites. Control of these invasive grasses will be necessary, but care will be needed to avoid negative impacts of control methods on natives.

**Key words:** *Cirsium arvense*, invasive cool-season grasses, prairie restoration, species richness, sustainability

## Implications for Practice

- There is no single best planting method for all situations: after 10 years, cover of planted, native nonplanted, and exotic species varied little among the three planting methods used in this study.
- Planting a higher richness seed mix results in reconstructions that harbor more species, but at the cost of lower proportional success.
- Patience can pay off: as the reconstructions matured, *Cirsium arvense* cover declined without herbicide application.
- Exotic cool-season grasses may be the biggest threat to these reconstructions: none of the planting methods or seed mix richness levels slowed their increase. Going forward, timing and intensity of prescribed fire will be priorities to address this problem.

## Introduction

As remnant tallgrass prairies become increasingly small and isolated in the Midwestern United States, prairie reconstruction from former agricultural land is seen as one of the few remaining hopes for sustaining this endangered ecosystem (Gerla et al. 2012). Properly established, these reconstructions can function to buffer and connect high quality remnants (Rowe et al. 2013), as well as provide ecosystem services, including habitat for prairie-dependent species, in their own right. Methods for

planting reconstructions that have high establishment and persistence of planted species and that resist infestation by noxious weeds (which by law in the United States must be controlled) are key to the success of this endeavor; reconstructions that require continued and expensive maintenance are unlikely to be sustainable.

Tallgrass prairie restoration (i.e. the enhancement of degraded remnant prairie) and prairie reconstruction (i.e. sowing prairie seed mixes in former agricultural fields) are not new practices, and much has been written about their outcomes. In particular, reconstructed prairies can improve resistance to invasive exotic plants (Blumenthal et al. 2005; Foster et al. 2015), create trajectories in many soil properties toward that of undisturbed prairie (Rosenzweig et al. 2016), and improve

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a variety of ecosystem functions (Foster et al. 2007). The time-course over which such benefits accrue and become comparable to remnant prairie is variable and in some cases stretches to centuries (Rosenzweig et al. 2016). Evaluation of the success of prairie reconstructions therefore can be seen as a moving target, depending on the end point of interest. Nonetheless, at the most basic and pragmatic level, a reconstruction in which planted species achieve and maintain dominance and weedy or noxious species are minimized will require little or no corrective maintenance, which is an important measure of success.

Studies of reconstructed prairies typically find declining planted species richness over time (Sluis 2002; Middleton et al. 2010; Willand et al. 2013). Most studies showing such changes use a chronosequence, in which prairie plantings of differing ages are compared to infer changes that occur over time. It is unclear how sensitive to subtle differences in year, site characteristics, and planting methods these inferences might be (e.g. Bakker et al. 2003). We have taken an experimental, geographically broad, long-term approach to the question of persistence of planted species, with an emphasis on comparing results of different planting methods (dormant-season broadcast, growing-season broadcast, and growing-season drill; hereafter DB, GB, and GD, respectively) and seed mix richness (10, 20, or 34 species) (Larson et al. 2011). At 5 years postplanting, Larson et al. (2011) reported that planted species richness was still increasing, but resistance to weedy exotics, including the noxious perennial *Cirsium arvense* L. (Larson et al. 2013), was unrelated to richness of the seed mix. Moreover, there were differences in establishment of perennial forbs (which were favored by the DB method) and warm-season grasses (favored by the GD method) among planting methods.

The current study reevaluates the experiment described in Larson et al. (2011) 5 years later (10 years postplanting). We ask if trends identified at 5 years postplanting for planted cover and richness, cover and richness of planted guilds, native non-planted cover, and exotic cover have changed in the intervening 5 years. Trends in frequency of noxious and other problematic species over time are examined as well. The primary goal of both this and the earlier study was to understand what influence early reconstruction practices have on long-term outcomes. These questions get at the practical issue of if or when, from a vegetation standpoint, a reconstruction has reached a stable state. Our focus is on vegetation, as others have found that soil processes take much longer to recover (Rosenzweig et al. 2016), but some studies have shown that planted species richness and cover may peak, and even begin to decline, within a decade (Hansen & Gibson 2014). At what point should a land manager take actions to e.g. augment species richness or spot spray invasive species, as opposed to allowing processes internal to the reconstruction to mature, and thereby potentially solve the perceived problem without intervention? An important component of management of prairie reconstructions is the frequency and timing of disturbance, especially prescribed fire. Because we wanted to compare effects of planting methods and seed mixes, it was not possible to also address fire effects, which were kept as consistent as possible across all sites, within our experimental design.

## Methods

### Study Sites

This study was conducted on fields formerly in a corn–soybean cropping rotation on U.S. Fish and Wildlife Service property at Neal Smith National Wildlife Refuge (NWR), Iowa (hereafter, Iowa sites,  $n = 3$ ); and Fergus Falls, Morris, and Litchfield Wetland Management Districts (WMDs), Minnesota (hereafter, Minnesota sites,  $n = 2$  per site, except at Fergus Falls WMD where one site was lost to other uses before the 2015 surveys). As in the earlier study of these reconstructed prairies (Larson et al. 2011), data from Minnesota and Iowa sites were analyzed separately because they used different seed sources and planting equipment. Growing-season precipitation (May–September) was variable, but generally below the long-term average during the early establishment period 2006–2009 (<http://www.ncdc.noaa.gov/cdo-web/>) in Minnesota and Iowa (Fig. S1, Supporting Information). Mean annual temperature is less variable than precipitation within Minnesota, ranging from 5.1°C (41.1°F) near Fergus Falls to 5.8°C (42.5°F) near Morris and 5.9°C (42.6°F) near Litchfield, MN; near Neal Smith Refuge, mean annual temperature is much higher, 10°C (50°F).

### Study Design

Treatments are described in detail, including the species in each seed mix, in Larson et al. (2011). Briefly, three planting methods (a dormant-season broadcasted seed application; a growing-season broadcasted seed application; and a growing-season drilled seed application) were fully crossed with low-, medium-, and high-richness mixes of 10, 20, and 34 species, respectively, and applied to twelve 12.2 × 12.2 m cells per study site. All the species in the low-richness mix were included in the medium-richness mix and all the species in the medium-richness mix were included in the high-richness mix. Each seed mix richness included representatives of four guilds (as defined by Brown [2004]): C<sub>3</sub> (cool-season) grasses (20% of seed mix by number), C<sub>4</sub> (warm-season) grasses (50%), legumes (10%), and nonlegume perennial forbs (20%; hereafter referred to as perennial forbs). Because we did not randomly assign species to richness levels, we cannot test effects of richness independent of species composition. We planted approximately 430 seeds/m<sup>2</sup>, regardless of richness of the mix, so the higher richness mixes had fewer seeds of each species. All fields were mowed (cut vegetation was not removed) once in early summer in 2005 and 2006 for control of annual weeds and were burned prior to green-up in spring 2009. All but one site was burned again in the dormant season prior to the 2015 surveys; a nonmetric multidimensional scaling (NMS) analysis for the 2015 matrix of species × plots did not separate the unburned site from the burned sites, so it was treated the same as the others in the analyses.

A 0.25 × 4 m subplot was randomly placed within a 2 × 6 m plot at the center of each treatment cell; here we visually estimated aerial cover of each species (total cover could therefore exceed 100%), bare ground, and litter once in mid-June through August 2005, 2006, 2007, 2010, and 2015. Species richness was

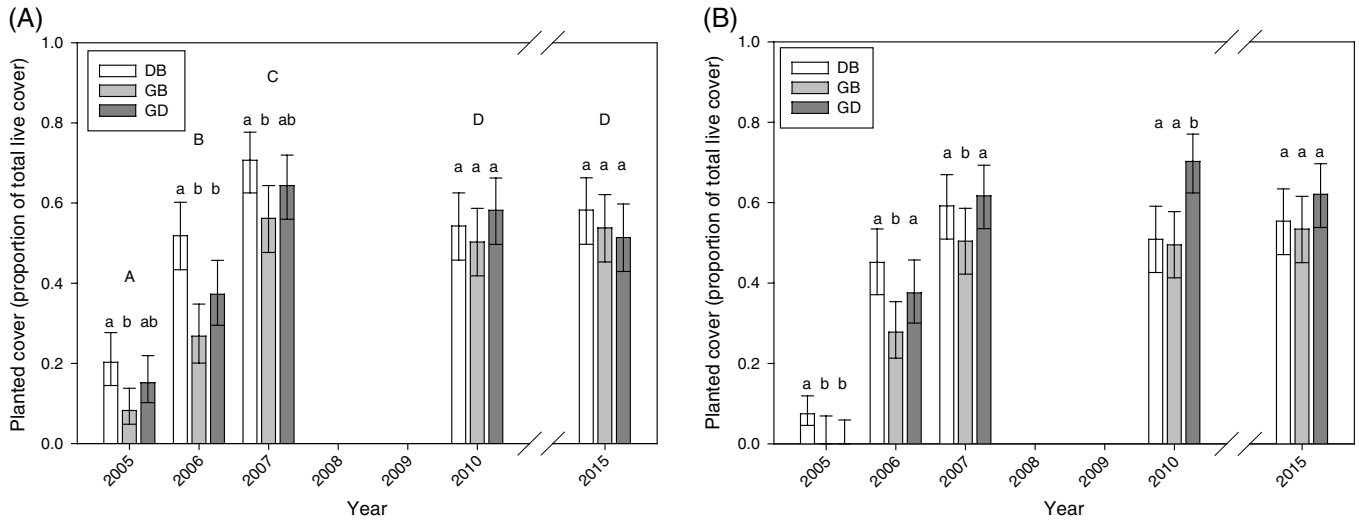


Figure 1. Cover of planted species at (A) Minnesota and (B) Iowa sites. Shown are least square means  $\pm$  95% CI for DB, GB, and GD planting methods as a function of survey year. Lowercase letters distinguish statistically different cover among planting methods within years. Uppercase letters distinguish statistically different mean planted cover between years in Minnesota, where the interaction between year and planting method was not significant.

evaluated on the  $2 \times 6$  m plot by counting all species encountered in the plot in 2007, 2010, and 2015. Field work began at the Iowa sites and progressed northward in an attempt to maintain a phenologically consistent sample across the eight fields.

#### Statistical Analysis

We used generalized linear mixed models (Proc GLMM in SAS version 9.4 (SAS Institute, Inc. (c) 2002–2012, Cary, NC, USA)) to evaluate the role of planting method and seed mix richness and their interaction on total planted cover and richness, cover and richness of individual guilds, total native cover that was not planted, total exotic cover, and cover of the noxious species *Cirsium arvense* (Canada thistle). The analysis was a randomized block design with repeated measures; each site was a random block, year was the repeated measure, and plots were subsamples nested within each site, planting method, and seed mix richness. Means within significant treatment effects were separated with Fisher's least significant difference (Milliken & Johnson 2002). Cover was expressed as a proportion of total live cover to standardize effects of growing conditions that varied by year, but see Table S1 for total live, planted, native nonplanted, and exotic cover per year. Richness was expressed as a proportion of the total number of species planted (or total number of species planted within each guild) that was observed; expression as a proportion makes it clearer when species were planted but did not establish. To better characterize individual species' responses, the proportion of plots in which each species was planted and established and the proportion of plots in which each species was not planted but to which it spread, were also calculated. The number of plots per year containing state-listed noxious species (per Plants.USDA.gov, accessed 5 Aug 2016) and other problematic species were tabulated and trends were plotted without statistical analysis.

## Results

#### Planted Species

Cover of planted species did not differ between 2010 and 2015 at both the Minnesota and Iowa sites (Table S2; Fig. 1). At the Minnesota sites, planted cover was highest (averaged over all years) in the DB plots (50%; all cover values are expressed as percentage of total live cover), lowest in the GB plots (35%), and intermediate in the GD plots (44%); there was no interaction with year. At Iowa sites, planting method interacted with year, but by 2015 all methods produced equivalent planted cover ( $\bar{x} = 57\%$ ). Planted species richness had no influence on cover of planted species in either Minnesota or Iowa sites.

Cover of planted cool-season grasses in both Minnesota and Iowa sites peaked in 2007 (32 and 29% at Minnesota and Iowa sites, respectively), after which their persistence was highly variable and cover was low (Table S2; Fig. S2). In contrast, in Minnesota, warm-season grass cover declined between 2010 and 2015 for each planting method while in Iowa, it declined only in the GD method (Table S2; Fig. S3). At the Minnesota sites, drilled forb cover continued to lag behind that in the broadcast methods in 2015 and all three planting methods produced greater forb cover in 2015 than in 2010 (Table S2; Fig. S4a). By 2015 at the Iowa sites, forb cover did not differ among the planting methods, but did increase with seed mix richness within each planting method (Table S2; Fig. S4b).

Proportion of planted species that established had a significant year by seed mix richness interaction in both Minnesota and Iowa sites (Table S2; Fig. 2). In each year, a larger proportion of the low-richness than higher richness species were recorded in Minnesota sites, but observed species richness declined between 2010 and 2015 in the low seed-mix richness plots and increased in the medium and high seed-mix richness plots. Iowa sites responded similarly, except that by 2015, due

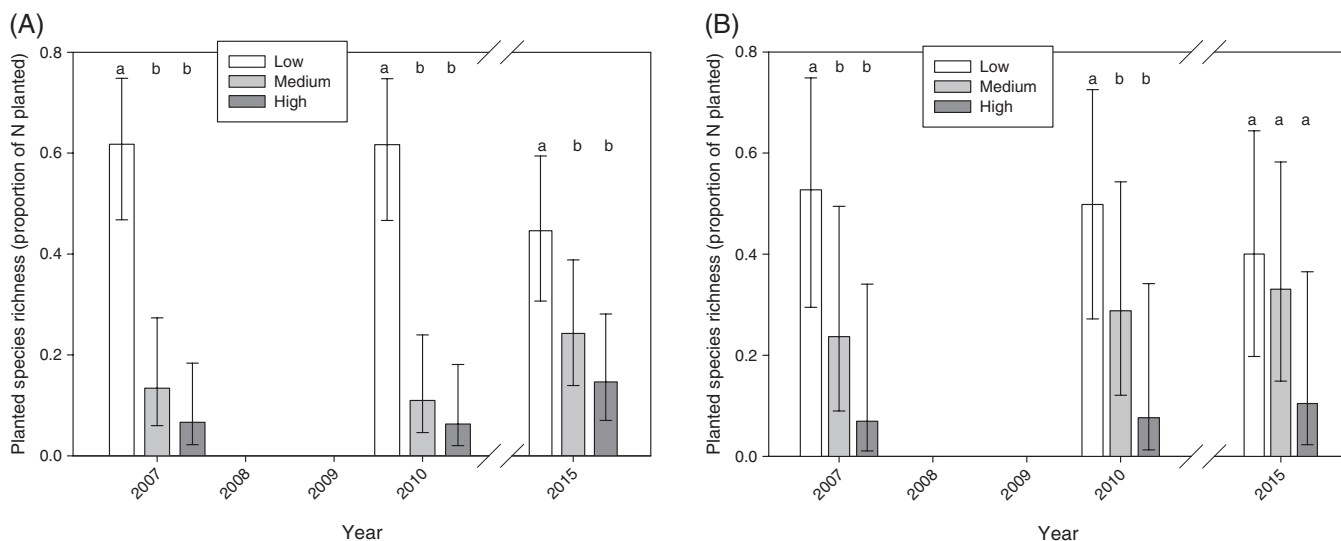


Figure 2. Richness of planted species at (A) Minnesota and (B) Iowa sites. Shown are least square means  $\pm$  95% CI for low, medium, and high seed-mix richness levels as a function of survey year. Lowercase letters distinguish statistically different planted species richness among seed mix richness levels within years.

to high variability, there was no statistical difference among the three seed mix richness treatments; observed species richness had declined between 2010 and 2015 on the low seed-mix richness plots but increased on the medium and high seed-mix richness plots.

Forbs made up most of the variation in species richness of our three seed mixes (see Table S3). Proportion of planted forb species observed was a three-way interactive function of planting method, seed mix richness, and year at Minnesota sites, while only the three main effects were significant at the Iowa sites (Table S2; Fig. S5a). The only increase in proportion of forb species observed between 2010 and 2015 in Minnesota sites was in the high seed-mix richness DB plots, where the proportion doubled from 17 to 34%. A larger proportion (albeit smaller absolute number) of planted forb richness was observed in the low and medium seed-mix richness plots, however, in each planting method. In stark contrast to the Minnesota sites, Iowa sites had a higher proportion of planted forb richness observed in medium and high seed-mix richness plots than in low; a higher proportion in GB and GD plots than in DB plots; and an increase between 2007 and 2010 and between 2010 and 2015 (Table S2; Fig. S5b).

### Nonplanted Species

Native nonplanted cover declined to a low, stable level at the Minnesota sites by 2007 and was not influenced by planting method or seed mix richness (Table S2; Fig. 3A). Native nonplanted cover at Iowa sites declined to a higher, but stable ( $\bar{x}$  = 22%) level by 2006, at which point there was no longer an effect of planting method (Table S2; Fig. 3B). Over all years, native nonplanted cover was greater in the low seed-mix richness plots than in plots that received the richer mixes in Iowa sites.

At the Minnesota sites, exotic cover reached its lowest point in 2007, in the DB plots, after which all three planting methods converged to equivalent levels ( $\bar{x}$  = 37%) in 2010 and 2015 (Table S2; Fig. 4A). Cover of the noxious exotic *Cirsium arvense*, having increased through 2007, declined to a low and stable level by 2010 (Table S2; Fig. S6), and the increase in plots occupied per year has declined from 10 per year from 2007–2010 to 6 per year from 2010–2015 (Fig. 5A). Frequencies of other noxious species occurring at the Minnesota sites (Fig. 5A) were similar in 2010 and 2015, but two problematic exotic cool-season grasses, *Poa pratensis* (Kentucky bluegrass) and *Bromus inermis* (smooth brome), continued to increase in distribution through 2015 (Fig. 5A). *Poa pratensis*, but not *B. inermis*, also increased in cover (Table S2). Total exotic cover at the Iowa sites reached its lowest point in 2007 (Table S2; Fig. 4B). Exotic cover did not vary on the GD plots between 2007 and 2015, but experienced a transient increase on the DB and GB plots in 2010. *Cirsium arvense* cover was never greater than 1% and did not vary by year or treatment (Table S2). Of the other noxious and problematic species at the Iowa sites (Fig. 5B), *P. pratensis* and *B. inermis* both increased in distribution between 2010 and 2015, while *Daucus carota* (Queen Anne's lace) declined. Cover of *B. inermis* and *P. pratensis* was not influenced by seed mix richness or planting method, and only *P. pratensis* cover increased over time (Table S2).

### Trends in Individual Planted Species

Only one planted species, *Carex bicknellii* (Bicknell's sedge), was never observed on any plot (Table S3). By 2015, two cool-season grasses (*Elymus trachycaulus*; slender wheatgrass and *Nassella viridula*; green needlegrass) and one forb (*Solidago speciosa*; showy goldenrod) were no longer found in plots at the Minnesota sites (though *S. speciosa* was found outside of

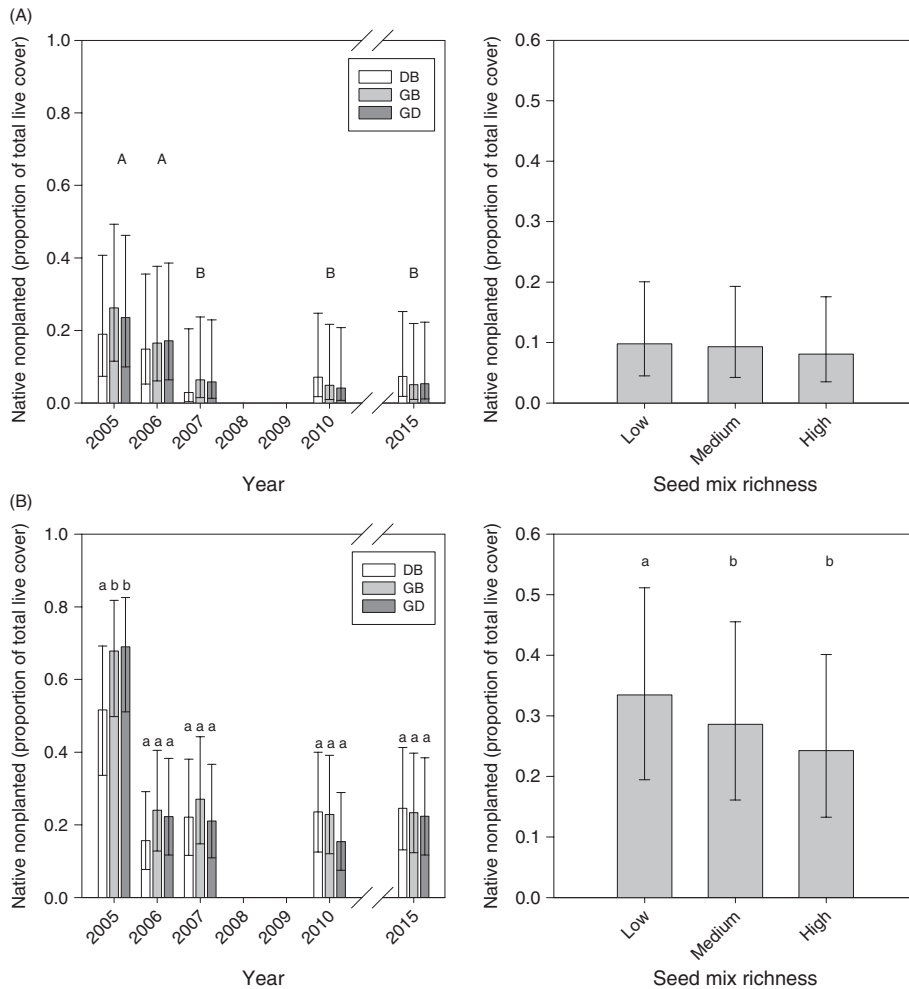


Figure 3. Cover of native nonplanted species at (A) Minnesota and (B) Iowa sites. Shown are least square means  $\pm$  95% CI for DB, GB, and GD planting methods as a function of survey year and for low, medium, and high seed-mix richness levels. Lowercase letters distinguish statistically different cover among planting methods within years. Uppercase letters distinguish statistically different mean planted cover between years in Minnesota, where the interaction between year and planting method was not significant. There also were no differences in native nonplanted cover among seed mix richness levels in Minnesota, but the graph is presented to facilitate comparison.

plots in at least one site). The same forb plus *Symphytotrichum laeve* (smooth blue aster) were lost from the Iowa sites, as well as the warm-season grass *Tridens flavus* (purpletop tridens; Table S3). *Andropogon gerardii* (big bluestem) was the most commonly encountered grass at both Minnesota and Iowa sites. *Monarda fistulosa* (beebalm) and *Oligoneuron rigidum* (stiff goldenrod) were found in greater than 90% of the plots in which they had been planted by 2015 at Minnesota sites. None of the forbs planted in the Iowa sites were this common, but *Zizia aurea* (golden alexander) and *Ratibida pinnata* (pinnate prairie coneflower) were found in at least 80% of plots in which they were planted. *Ratibida pinnata* was also very likely to have spread to plots where it was not planted in Iowa; its congener, *R. columnifera* (upright prairie coneflower), showed no such tendency in Minnesota, and in fact had declined substantially there by 2015. *Oligoneuron rigidum* was the most likely forb to spread beyond the plots in which it was planted in

Minnesota, and showed moderate tendencies to spread in Iowa. It is, of course, not possible to distinguish between planted and dispersed species that were in all three seed mixes.

## Discussion

Overall planted cover, native nonplanted cover, and exotic cover changed very little between 2010 and 2015. The peak in planted cover in 2007 in Minnesota was likely related to cool-season grasses, which flourished during the first few years but declined dramatically between 2007 and 2010. The peak in cover in 2010 in Iowa sites was clearly related to a peak in drilled warm-season grasses, which then declined to the level of those in broadcast plots by 2015. Unlike other studies that have varied seed mix richness (Bullock et al. 2007; Piper et al. 2007), this did not influence cover (as proxy for production) of planted species at our sites. Higher richness seed mixes also did not typically

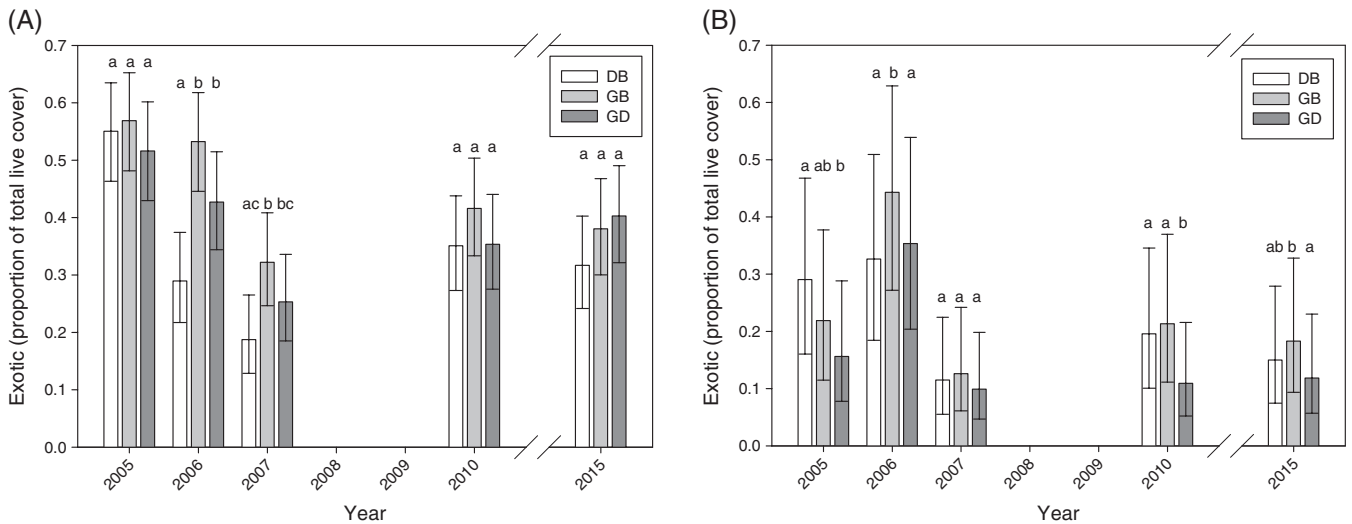


Figure 4. Cover of exotic species at (A) Minnesota and (B) Iowa sites. Shown are least square means  $\pm$  95% CI for DB, GB, and GD planting methods as a function of survey year. Lowercase letters distinguish statistically different mean cover among planting methods within years.

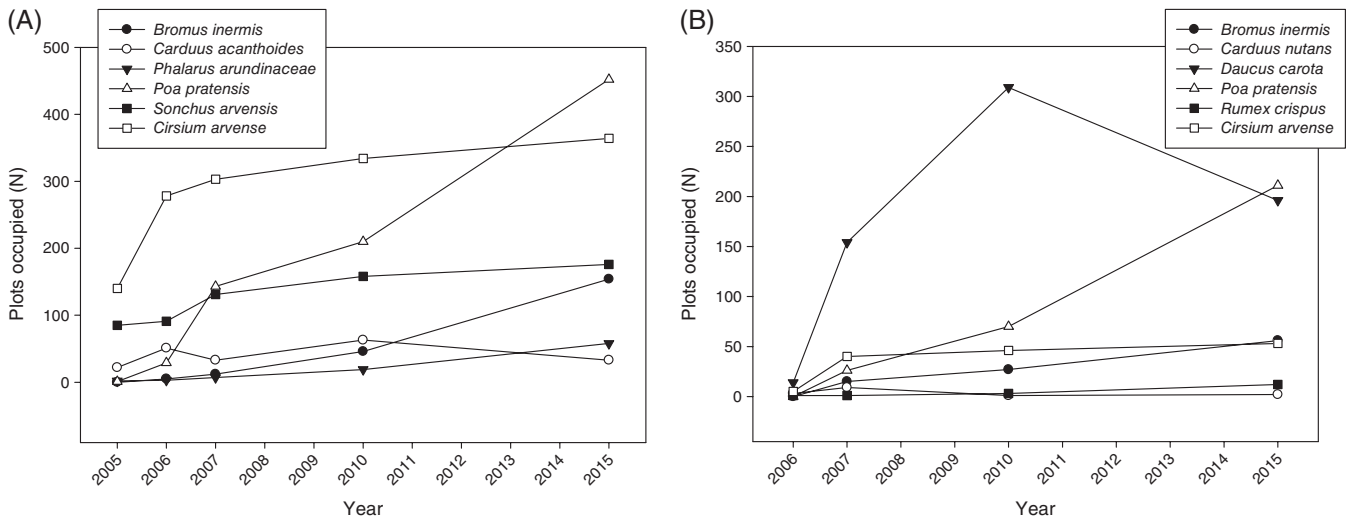


Figure 5. Trends in noxious and other problematic species at (A) Minnesota and (B) Iowa sites. Shown are counts of total plots occupied over time.

reduce cover of nonplanted species, except for native species at the Iowa sites. In contrast, Lepš et al. (2007) found reduced colonization in their 14-species compared to 4-species plantings at sites across Europe. The richness of seed mixes employed in reconstructions has increased over time, reaching into the hundreds of species in a recent report (Gerla et al. 2012). Future research will need to examine effects of the full range of seed mix richness levels being used.

The three planting methods in this study produced generally similar cover and species richness 10 years after planting. Cover of the noxious weed *Cirsium arvense*, which would trigger a mandatory management response, was likewise present only at low levels from 2010 to 2015, having declined from peaks in 2006 to 2007 at Minnesota sites in the absence of any herbicide treatment. Interestingly, unlike cover, frequency of *C. arvense* across plots in Minnesota did not

decline, suggesting that clones persisted, but had become less robust.

In contrast, the details of the planted guilds' cover and richness were in some cases still quite dynamic in 2015. Forbs in particular were still increasing in cover and richness, though not evenly among planting methods or planted richness levels. Because seed numbers per species declined as richness of the seed mix increased, it is to be expected that species in the higher richness mixes should appear less frequently, and this may partially account for the lower proportion of species observed in the higher richness mixes (Long et al. 2014; Grman et al. 2015). Nonetheless, most species, even in the highest richness mix, established over the 10 years of the study and cover was not negatively affected by lower number of seeds per species in high richness mixes. This suggests that, within the richness limits of our seed mixes, planted cover will not decline as a result

of slower or limited establishment of some species in higher diversity mixes. Even species that established well early on, but have declined, may have been crucial in reducing infestation of exotic species while the more durable, but slower-to-establish, native species gained momentum (Larson et al. 2013). On the other hand, species that failed to establish, or have struggled over the entire 10-year period at both Minnesota and Iowa sites (e.g. *Liatris aspera*; tall blazingstar), may require greater or different management inputs or different microsites for establishment than were available. Failure of a species from a single seed source may simply reflect upon that source, but failure from differently sourced seed suggests the species has more specific germination or establishment requirements than are available (e.g. mycorrhizal fungi) or provided (e.g. rhizobial inoculum), or require time, fire, or other physical treatment to break dormancy (Baskin & Baskin 2004). Because seeds are among the most expensive components of prairie reconstruction, research that helps practitioners make wise choices of species likely to establish is much needed. Some requirements for germination and establishment, however, relate to weather conditions over which practitioners have no control. Because our treatments were all planted in the same year, we cannot evaluate such year-effects, although others have found them to be strong (Bakker et al. 2003). Wilson (2015) e.g. suggested planting over several years to increase chances of having at least 1 year with good establishment conditions, assuming seed costs are high and planting costs are low.

Five years after planting, Larson et al. (2011) concluded that better results were obtained by drilling if planting during the growing season, but if broadcasting seed, the dormant season was preferable. Ten years after planting, our recommendations have changed very little, although the differences among planting methods are generally fewer than they were 5 years ago. At the Minnesota sites, a DB seeding always produced as good or better cover and richness as other planting methods. The GB method had reduced cover and richness of warm-season grasses, but was otherwise equivalent to the other methods. Forb cover (and proportional richness on the medium seed-mix richness plots) was lower when seed was drilled during the growing season. At the Iowa sites, proportion of planted forb species observed on DB plots was lower than on either GB or GD plots, a somewhat surprising result (Liegel & Lyon 1986; Rowe 2010). Planted forb cover did not vary among planting methods though, perhaps suggesting that one (or more) species was especially favored by the DB method and its prevalence may have suppressed richness. No other differences in cover or richness could be attributed to planting method at the Iowa sites.

Two results in 2015 are reasons for concern: cover of planted species was only slightly over 50%, and the cool-season exotic grasses *Poa pratensis* and *Bromus inermis* were increasing at both Minnesota and Iowa sites. Even including nonplanted native species, native cover averaged less than 60% at Minnesota sites, but approached a more respectable 80% at Iowa sites. That these numbers appear to be stable is encouraging, but the increase in the cool-season grasses may erode them over time (Grant et al. 2009; Larson & Larson 2010),

especially if disturbance is not imposed (Murphy & Grant 2005). None of our treatment combinations had any effect on *P. pratensis* cover. Although we did not assess this statistically (the plotted data are simply counts of plots occupied), it appears that both exotic grasses were increasing prior to the decline in the planted cool-season grasses in 2010, suggesting that the presence of a similar functional group did not suppress these problematic invaders. We note, however, that by far the most abundant planted cool-season grasses were *Elymus* species, which, though good competitors (Ulrich & Perkins 2014), generally are not long-lived (Liegel & Lyon 1986). Other planted cool-season grasses such as *Nassella viridula* failed to establish in numbers that could have been expected to compete with *P. pratensis* or *B. inermis*. Demographic studies that pinpoint the limiting stage in establishment of more long-lived and competitive native cool-season grasses (James et al. 2011) may provide a way forward for encouraging cool-season native cover and reducing invasion by these aggressive exotic grasses.

Postseeding management actions were intentionally standardized across these study sites, which limits our ability to address this important aspect of prairie reconstruction. Prescribed fire, in particular, is a valuable management tool for both remnant and reconstructed prairies (Bowles & Jones 2013). Reconstructions in this study were burned during the dormant season, a practice that has been shown to reduce diversity in restorations in Illinois (Copeland et al. 2002) and Michigan (Heslinga & Grese 2010) but is used less often in Minnesota where effects have not been documented in the published literature. An obvious next step is to vary timing and frequency of fire within our study sites, where richness is still increasing, in an effort to understand how to promote maximum expression of planted species.

In conclusion, we find that in many respects these reconstructions have reached a stable state, at least in terms of cover of planted and nonplanted species. At this point, if noxious species exceed acceptable levels (with the possible exception of *Daucus carota* which may continue to decline in site occupancy) management actions seem appropriate. Because planted forb richness is still increasing under some of the treatments, care would need to be taken with any action to avoid harming forbs that are still establishing. This is a special concern with respect to the invasive cool season grasses; if they are not controlled, past experience suggests they will gradually suppress the native species (Cully et al. 2003; Grant et al. 2009; Ulrich & Perkins 2014). To reduce abundance of these aggressive grasses, however, often requires repeated treatments of fire and/or herbicide (Willson & Stubbendieck 1997; Bahm et al. 2011) that also have the potential to reduce native richness. Given the fragmented status of both remnant and reconstructed prairies, management actions (e.g. fire or grazing) will always be necessary to retain grassland structure and diversity. Results of this study indicate that management to control many noxious weeds in the early stages of reconstruction may be unnecessary, however, as the planted species gain dominance over time and limit their spread.

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## LITERATURE CITED

- Bahm MA, Barnes TG, Jensen KC (2011) Herbicide and fire effects on smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*) in invaded prairie remnants. *Invasive Plant Science and Management* 4:189–197
- Bakker JD, Wilson SD, Christian JM, Li XD, Ambrose LG, Waddington J (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications* 13:137–153
- Baskin JM, Baskin CC (2004) A classification system for seed dormancy. *Seed Science Research* 14:1–16
- Blumenthal DM, Jordan NR, Svenson EL (2005) Effects of prairie restoration on weed invasions. *Agriculture, Ecosystems & Environment* 107:221–230
- Bowles ML, Jones MD (2013) Repeated burning of eastern tallgrass prairie increases richness and diversity, stabilizing late successional vegetation. *Ecological Applications* 23:464–478
- Brown CS (2004) Are functional guilds more realistic management units than individual species for restoration? *Weed Technology* 18:1566–1571
- Bullock JM, Pywell RF, Walker KJ (2007) Long-term enhancement of agricultural production by restoration of biodiversity. *Journal of Applied Ecology* 44:6–12
- Copeland TE, Sluis W, Howe HF (2002) Fire season and dominance in an Illinois tallgrass prairie restoration. *Restoration Ecology* 10:315–323
- Cully AC, Cully JF, Hiebert RD (2003) Invasion of exotic plant species in tallgrass prairie fragments. *Conservation Biology* 17:990–998
- Foster BL, Murphy CA, Keller KR, Aschenbach TA, Questad EJ, Kindscher K (2007) Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. *Restoration Ecology* 15:652–661
- Foster BL, Houseman GR, Hall DR, Hinman SE (2015) Does tallgrass prairie restoration enhance the invasion resistance of post-agricultural lands? *Biological Invasions* 17:3579–3590
- Gerla PJ, Cornett MW, Ekstein JD, Ahlering MA (2012) Talking big: lessons learned from a 9000 hectare restoration in the northern tallgrass prairie. *Sustainability* 4:3066–3087
- Grant TA, Flanders-Wanner B, Shaffer TL, Murphy RK, Knutsen GA (2009) An emerging crisis across northern prairie refuges: prevalence of invasive plants and a plan for adaptive management. *Ecological Restoration* 27:58–65
- Grman E, Bassett T, Zirbel CR, Brudvig LA (2015) Dispersal and establishment filters influence the assembly of restored prairie plant communities. *Restoration Ecology* 23:892–899
- Hansen MJ, Gibson DJ (2014) Use of multiple criteria in an ecological assessment of a prairie restoration chronosequence. *Applied Vegetation Science* 17:63–73
- Heslinga JL, Grese RE (2010) Assessing plant community changes over sixteen years of restoration in a remnant Michigan tallgrass prairie. *American Midland Naturalist* 164:322–336
- James JJ, Svejcar TJ, Rinella MJ (2011) Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* 48:961–969
- Larson DL, Larson JL (2010) Control of one invasive plant species allows exotic grasses to become dominant in northern Great Plains grasslands. *Biological Conservation* 143:1901–1910
- Larson DL, Bright JB, Drobney P, Larson JL, Palaia N, Rabie PA, Vacek S, Wells D (2011) Effects of planting method and seed mix richness on the early stages of tallgrass prairie restoration. *Biological Conservation* 144:3127–3139
- Larson DL, Bright JB, Drobney P, Larson JL, Palaia N, Rabie PA, Vacek S, Wells D (2013) Using prairie restoration to curtail invasion of Canada thistle: the importance of limiting similarity and seed mix richness. *Biological Invasions* 15:2049–2063
- Lepš J, Dolezal J, Bezemer TM, Brown VK, Hedlund K, Igual AM, et al. (2007) Long-term effectiveness of sowing high and low diversity seed mixtures to enhance plant community development on ex-arable fields. *Applied Vegetation Science* 10:97–110
- Liegel K, Lyon J (1986) Prairie restoration program at the International Crane Foundation. Pages 190–194 In: Clamby G, Pembel R, (eds) *Proceedings of the Ninth North American Prairie Conference*, Fargo, ND
- Long Q, Foster BL, Kindscher K (2014) Seed and microsite limitations mediate stochastic recruitment in a low-diversity prairie restoration. *Plant Ecology* 215:1287–1298
- Middleton EL, Bever JD, Schultz PA (2010) The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. *Restoration Ecology* 18:181–187
- Milliken GA, Johnson DE (2002) *Analysis of Messy Data*. Chapman and Hall/CRC, New York
- Murphy RK, Grant TA (2005) Land management history and floristics in mixed-grass prairie, North Dakota, U.S.A. *Natural Areas Journal* 25:351–358
- Piper JK, Schmidt ES, Janzen AJ (2007) Effects of species richness on resident and target species components in a prairie restoration. *Restoration Ecology* 15:189–198
- Rosenzweig ST, Carson MA, Baer SG, Blair JM (2016) Changes in soil properties, microbial biomass, and fluxes of C and N in soil following post-agricultural grassland restoration. *Applied Soil Ecology* 100:186–194
- Rowe HI (2010) Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. *Restoration Ecology* 18:253–262
- Rowe HI, Fargione J, Holland JD (2013) Prairie restorations can protect remnant tallgrass prairie plant communities. *The American Midland Naturalist* 170:26–38
- Sluis WJ (2002) Patterns of species richness and composition in re-created grassland. *Restoration Ecology* 10:677–684
- Ulrich E, Perkins L (2014) *Bromus inermis* and *Elymus canadensis* but not *Poa pratensis* demonstrate strong competitive effects and all benefit from priority. *Plant Ecology* 215:1269–1275
- Willand JE, Baer SG, Gibson DJ, Klopff RP (2013) Temporal dynamics of plant community regeneration sources during tallgrass prairie restoration. *Plant Ecology* 214:1169–1180
- Willson GD, Stubbendieck J (1997) Fire effects on four growth stages of smooth brome (*Bromus inermis* Leys.). *Natural Areas Journal* 17:306–312
- Wilson SD (2015) Managing contingency in semiarid grassland restoration through repeated planting. *Restoration Ecology* 23:385–392

## Supporting Information

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

**Figure S1.** Departure from long-term mean growing season (May–September) rainfall at study sites.



**Figure S2.** Cover of planted cool-season grasses.

**Figure S3.** Cover of planted warm-season grasses.

**Figure S4.** Cover of planted forbs.

**Figure S5.** Proportion of planted forb species observed in surveys.

**Figure S6.** Cover of *Cirsium arvense* as a function of planting method and year.

**Table S1.** Mean  $\pm$  SE percent cover estimates by year at Minnesota and Iowa study sites.

**Table S2.** Results of statistical tests.

**Table S3.** Proportion of plots occupied by planted species.

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