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RESEARCH ARTICLE

Seed mix design and first year management influence multifunctionality and cost-effectiveness in prairie reconstruction

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Agricultural intensification continues to diminish many ecosystem services in the North American Corn Belt. Conservation programs may be able to combat these losses more efficiently by developing initiatives that attempt to balance multiple ecological benefits. In this study, we examine how seed mix design and first year management influence three ecosystem services commonly provided by tallgrass prairie reconstructions (erosion control, weed resistance, and pollinator resources). We established research plots with three seed mixes, with and without first year mowing. The grass-dominated "Economy" mix had 21 species and a 3:1 grass-to-forb seeding ratio. The forb-dominated "Pollinator" mix had 38 species and a 1:3 grass-to-forb seeding ratio. The grass:forb balanced "Diversity" mix, which was designed to resemble regional prairie remnants, had 71 species and a 1:1 grass-to-forb ratio. To assess ecosystem services, we measured native stem density, cover, inflorescence production, and floral richness from 2015 to 2018. The Economy mix had high native cover and stem density, but produced few inflorescences and had low floral richness. The Pollinator mix had high inflorescence production and floral richness, but also had high bare ground and weed cover. The Diversity mix had high inflorescence production and floral richness (comparable to the Pollinator mix) and high native cover and stem density (comparable to the Economy mix). First year mowing accelerated native plant establishment and inflorescence production, enhancing the provisioning of ecosystem services during the early stages of a reconstruction. Our results indicate that prairie reconstructions with thoughtfully designed seed mixes can effectively address multiple conservation challenges.

Key words: ecosystem services, erosion control, pollinators, prairie reconstruction, seedling establishment, tallgrass prairie, weed resistance

Implications for Practice

- Seed mixes designed to concurrently balance ecosystem functions of native plant cover and biodiversity/wildlife benefits are more cost-effective than seed mixes designed to maximize single services.
- Tallgrass prairie reconstructions should be mowed during the initial year of establishment to reduce annual weed competition and accelerate and enhance ecosystem service provision.
- Seed mix cost is not necessarily a good predictor of ecological outcomes—land managers should apply knowledge of regionally appropriate target plant communities to achieve desired ecological outcomes with high cost-effectiveness.

Introduction

Land use intensification and rising production inputs continue to diminish many ecosystem services in the North American Corn Belt. Reduced pollinator abundance (Cameron et al. 2011; Koh et al. 2016), deteriorating water quality (Jones et al. 2018), and soil erosion (Wright & Wimberly 2013) have all become large-scale stressors facing ecosystems in these agricultural landscapes. In response, organizations have developed targeted programs to address specific conservation challenges. For example, the Conservation Reserve Program (CRP) has created several conservation practices (CPs) designed to enhance single ecosystem services, such as the upland game bird provision (CP33—Habitat buffers for upland birds), erosion control (CP2—Establishment of permanent native grasses), and flood control (CP23—Wetland restoration on floodplains) (United States Department of Agriculture 2018*a*). An especially popular initiative in recent years has been the restoration of pollinator habitat (CP42). Approximately 160,000 ha have been dedicated

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to pollinator habitat plantings in Corn Belt states (United States Department of Agriculture 2018*b*). However, given trends in reduced funding for conservation (Classen 2014), future initiatives may need to increase the efficiency with which they address conservation challenges. Conservation programs may be able to achieve greater impact with limited resources (i.e. be more cost-effective) by designing initiatives that attempt to balance multiple ecological benefits.

Previous research has shown that diverse ecosystems provide a wide variety of ecological benefits simultaneously (Macfadyen et al. 2012; Wratten et al. 2012). Productivity, rates of nutrient cycling, nutrient capture, and decomposition, and the stability of ecosystem services all tend to be positively correlated with community diversity (reviewed in Cardinale et al. 2012). In the Midwestern United States specifically, species-rich tallgrass prairies provide several ecosystem services when restored on the landscape (Asbjornsen et al. 2014; Schulte et al. 2017). For example, strategically reconstructing tallgrass prairie on 10% of agricultural fields can reduce N and P losses by up to 82% (Zhou et al. 2014). Further, integrating prairie into agricultural fields and other parts of the rural landscape can reduce sediment runoff (Helmers et al. 2012), increase pollinator abundance (Ries et al. 2001; Schulte et al. 2017), and increase bird species richness (Schulte et al. 2017). While the multiple ecological benefits of tallgrass prairie are well known, few studies have examined cost-effectiveness in prairie reconstruction by considering the ecological benefits provided per unit project cost.

Seed mix design is the biggest determinant of project costs and ecological outcomes in prairie reconstruction (Larson et al. 2011, 2017; Grman et al. 2013; Phillips-Mao et al. 2015). One aspect of seed mix design that is particularly influential for costs and outcomes is the grass-to-forb seeding ratio (based on number of seeds sown). From a cost perspective, seed mixes with a high grass-to-forb ratio are less expensive than seed mixes with a low grass-to-forb ratio because grass seed is generally less expensive than forb seed. However, designing mixes in which the seeding rate of one functional group is either too high or too low can adversely affect specific ecological outcomes. For example, seed mixes in which the grass seeding rate is too high can produce grass-dominated stands where forbs establish poorly and do not persist (Dickson & Busby 2009; McCain et al. 2010; Török et al. 2010; Valkó et al. 2016); ultimately, these stands have little value as pollinator habitat (Hopwood 2008). Conversely, seed mixes in which the grass seeding rate is too low can produce stands with low cover (i.e. high amounts of bare ground); these stands are highly susceptible to weed invasion and provide less protection against soil erosion and water quality degradation (Boyd 1942; Ellison 1950; Burke & Grime 1996). Another aspect of seed mix design that influences costs and outcomes is species selection. A customized seed mix, in which species' moisture tolerances are matched to site soil conditions, should produce stands that establish readily and persist long term (Smith et al. 2010). Many reconstruction projects simply use "off-the-shelf" seed mixes designed to achieve specific program goals. When a seed mix contains species that perform poorly under local soil conditions overall cost-effectiveness declines.

First year management can also influence the costs and outcomes of prairie reconstruction. Fast-growing, annual weeds are a common problem in post-agricultural sites where many prairie reconstructions occur. If these annual weeds establish and become dominant before the prairie seeds germinate, they can delay or reduce native establishment, reduce native diversity, and increase long-term management costs (Schramm 1990; Blumenthal et al. 2003). Previous research suggests that mowing promotes prairie plant establishment by increasing light availability to developing seedlings. For example, Williams et al. (2007) found that frequent mowing promotes the establishment of forbs sown into warm-season prairie grass stands. The impact of this management was long-standing as forb abundance remained higher in mowed plots than in control plots 10 years later (Williams et al. 2010). Because the seed costs of a reconstruction project can be 15 times greater than the cost of establishment mowing (Phillips-Mao et al. 2015), a significant increase in seedling survival would represent a large increase in cost-effectiveness.

In this study, we test whether prairie reconstructions installed at post-agricultural sites can effectively provide three ecosystem services (erosion control, weed resistance, and pollinator resources) and assess whether seed mix design and first year mowing influence the degree of service enhancement. We established research plots with three different seed mixes, both with and without first year mowing. The seed mixes differed in diversity, grass-to-forb seeding ratio, degree of soil type customization, and cost. To assess the ecosystem services provided by each seed mix × mowing treatment combination, we measured native species richness, stem density (of native grasses and native forbs), cover (native plants, annual weeds, perennial weeds, and bare ground), inflorescence production, and floral richness. To evaluate cost-effectiveness, we considered the cost of project materials (i.e. native seeds planted) with respect to the ecosystem services it provided.

Methods

Study Site

We conducted this study at the Iowa State University Northeast Research and Demonstration Farm near Nashua, Iowa (42°56′N, 92°34′W). The site is relatively level with slopes not exceeding a 5% grade. Soil composition is primarily poorly drained Clyde clay loams with a minor component of somewhat poorly drained Floyd loams (Natural Resources Conservation Service 2019). Sub-surface tile drains exist on site and are spaced approximately 18–24 m apart. The land was used for corn and soybean production prior to site establishment in 2015.

To prepare the research area, we seeded the site with soybeans prior to research plot establishment. We applied a pre-emergent herbicide (pyroxasulfone) in May 2014 at a rate of 0.179 kg/ha and a post-emergent herbicide (glyphosate) in mid-July at a rate of 1.094 kg/ha. To create a suitable seedbed, we chisel-plowed the site in March 2015 and field cultivated the site twice in April 2015. The prepared seedbed was loose, with clods less than 6.4 mm in diameter. To stabilize the soil as prairie seedlings established, we seeded a nurse crop of oats at a rate of 36.3 kg/ha.

Seed Mixes

We established plots with three different seed mixes: (1) the "Economy mix"—21 species at a 3:1 grass-to-forb seeding ratio (assessed on the basis of seed numbers) (Table S1); (2) the "Pollinator mix"—38 species at a 1:3 grass-to-forb seeding ratio (Table S2); and (3) the "Diversity mix"—71 species at a 1:1 grass-to-forb seeding ratio (Table S3). The Economy mix was designed to resemble a seed mix that met the specifications for USDA's Rare and Declining Habitat Conservation Practice (CP25). The goals of CP25 are varied and include: providing wildlife habitat (resources for nesting, escape cover, and food), erosion control, and pollinator resources (United States Department of Agriculture 2015). The Pollinator mix was designed to resemble a seed mix that met the specifications for USDA's Pollinator Habitat Conservation Practice (CP42), the goals of which are to provide high-quality habitat for pollinators throughout the growing season (United States Department of Agriculture 2011). The Diversity mix was designed to resemble a remnant prairie of matching geographic and soil conditions on site (i.e. species included in the mix would be expected to exist on mesic prairie remnants in the Iowan Surface ecoregion, United States Environmental Protection Agency 2013, and were commercially available). The costs of the Economy, Pollinator, and Diversity mixes in 2015 were $321, $909, and $719 per hectare, respectively.

We purchased seed from native seed nurseries in Iowa and adjacent states in January 2015. Seeds were stored at 4°C and 45% relative humidity prior to planting. To ensure accuracy in seeding rates and seed purity, we calculated seeding rates for each species using pure live seed (PLS). We standardized the overall seeding rate of each mix to approximately 430 PLS/m^2. We weighed, bagged, and mixed the seed for each plot separately.

Experimental Design

We established 36 research plots using a split-plot design with two spatial blocks. Eighteen plots (6.1 × 8.53–m each) were established in each block. Within each block, we randomly established three replicate plots of each seed mix in 12.2 × 8.53–m strips and the mowing treatment was applied to one randomly selected half of each strip. This resulted in an overall experimental design of 3 seed mixes × 2 mowing treatments × 3 replicates × 2 blocks = 36 research plots (Fig. S1). Because of minor flooding during a critical establishment time, plot 18 (SE corner of block 2, Fig. S1) was excluded from analyses.

We drill-seeded the research plots in April 2015. Drilling was unidirectional to eliminate seed contamination between adjacent plots. We seeded each plot independently using a Truax FLX-86U no-till drill (Truax Company, Inc., New Hope, MN, U.S.A.) with a John Deere JD-5325 tractor. To minimize contamination between seed mixes, we cleaned the drill after seeding each plot.

First Year Management

We applied a first year (2015) mowing treatment to half of the plots of each seed mix. When the vegetation height exceeded 50 cm, we mowed it to a height of 11.4 cm using a riding type rotary mower. We mowed the plots four times in 2015 (16 June, 23 July, 13 August, 4 November) and all remaining thatch was left on site. We did not mow in 2016, 2017, or 2018.

Data Collection

In each year of the study (2015–2018), we measured stem density of planted species in August (September for first year sampling). We assessed the stem density of planted species in five 0.1 m^2 quadrats in each plot. We placed quadrats at 1-m intervals along a 5-m transect established at a random position within each plot. We randomized transect location each year. To minimize edge effects, we did not place quadrats within 1 m of plot edges. In each quadrat, we identified and counted all stems (ramets) greater than 10 cm in height of each planted species. We recorded native species richness as the total number of planted native species present within the surveyed quadrats of each plot.

We measured canopy cover of native plants, annual weeds, perennial weeds, and bare ground in the same quadrats used to assess stem density and species richness. We visually estimated cover for these classes to the nearest 5%. We also recorded the number of inflorescences and floral richness (number of planted species that produced inflorescences) of species rooted in the quadrat. Due to the broad phenological range of species planted in this study, we included emerging buds and filled seed heads in our inflorescence counts in order to ensure floral resource estimation over the entire growing season. We excluded seed heads that were damaged or mostly dispersed from our counts in order to avoid double counting standing inflorescences from previous years. We did not count inflorescences from unplanted species. We measured cover, inflorescence number, and floral richness each year from 2016 to 2018. We report inflorescence number as the total number of native planted inflorescences produced from 2016 to 2018 and floral richness as the total number of native planted species that produced inflorescences from 2016 to 2018.

We used stem density, cover, floral richness, and inflorescence production to assess the ecosystem services (erosion control, weed resistance, and pollinator resources) provided by each seed mix. Previous studies have shown that stem density and cover are key determinants of erosion resistance (Boyd 1942; Ellison 1950; Durán Zuazo & Rodríguez Pleguezuelo 2008), that prairie reconstructions with low establishment are more susceptible to weed invasion (Middleton et al. 2010; Carter & Blair 2012; Nemec et al. 2013), and that inflorescence number and floral richness influence pollinator habitat quality (Hopwood

2008; Pywell et al. 2011). In accordance with these previous studies, we used native stem density and native cover to assess erosion control, bare ground cover and weed cover to assess weed resistance, and cumulative inflorescence production and floral richness to assess pollinator resources.

We assessed the cost-effectiveness of each seed mix × mowing treatment combination in two ways: the cost of producing 1,000 native stems and the cost of producing 1,000 native inflorescences. Cost-effectiveness was calculated as the cost of the seed mixture (per plot) divided by the variable of interest (i.e. the number of 1K native stems produced in 2018 or the number of 1K inflorescences produced between 2016 and 2018) per plot.

Data Analysis

We analyzed stem density, species richness, and cover using repeated measures analysis of variance (ANOVA), with seed mix and mowing as fixed factors, year as the repeated measure, and plot nested within block as a random factor. We analyzed the total cumulative number of inflorescences produced by 2018 (2016–2018) and cost-effectiveness using two-way ANOVA with seed mix and mowing as fixed factors and plot nested within block as a random factor. To meet the assumptions of normality and homoscedasticity of residual variance, grass stem density, forb stem density, and annual weed cover were cube-root transformed, perennial weed cover was $\log(y+0.1)$ transformed, bare ground cover was square $\text{root}(y+0.1)$ transformed, cumulative inflorescence production was log-transformed, and the cost of producing 1,000 native stems was 1/square root-transformed. Within year post hoc comparisons of significant treatment effects were made using one-way ANOVA and Tukey HSD tests. All data were analyzed in R (v. 3.5.1, R Core Team 2018).

Data Visualization

To assess multifunctionality, we scored each seed mix on their ability to achieve the three ecosystem services examined in this study. To assess quality of pollinator habitat, we used inflorescence production (total inflorescences produced, 2016–2018) and floral richness (total species that produced inflorescences, 2016–2018). To assess weed resistance, we used weed cover^{-1} (in 2018) and bare ground cover^{-1} (in 2018). To assess erosion control, we used percent native cover (in 2018) and native stem density (in 2018). We used native cover as our proxy for erosion control, rather than total cover, because weeds are generally viewed as undesirable in prairie reconstructions, because the root systems of weeds are not as expansive as the root systems of prairie plants, and because any noxious weeds would need to be removed from reconstructions, thereby negating their value for erosion control. The seed mix with the highest value for each variable was scored as a 1.0 and the other seed mixes were scored as a relative proportion of that total (i.e. highest possible multifunctionality score = 6.0). For clarity, we presented each seed mix's multifunctionality score as a percentage out of 100. We depicted the relative values of each seed mix as a "multifunctionality flower," in which each of the six traits was represented as a petal (see Asbjornsen et al. 2014 for comparable analysis).

Results

Species Richness

Species richness differed between seed mixes (Table S4). The Diversity mix had higher species richness than the Pollinator and Economy mixes in all 4 years of the study and the Economy mix had higher species richness than the Pollinator mix in 2015 and 2017 (Fig. 1A). First year management influenced species richness; however, this effect became less pronounced with time (Table S4). Species richness was higher in mowed plots than in plots that were not mowed in 2015 and 2016, but not in 2017 and 2018 (Fig. 1D). Species richness changed with time (Table S4) and was generally lower in earlier years (2015 and 2016) than later years (2017 and 2018) (Fig. 1A and 1D).

Stem Density

Native grass and native forb stem density differed between seed mixes (Table S4). Grass stem density was higher in the Economy and Diversity mixes than in the Pollinator mix (Fig. 1B), while forb stem density was higher in the Diversity and Pollinator mixes than in the Economy mix in most years (Fig. 1C). Grass and forb stem density were higher in mowed plots than in plots that were not mowed (Table S4); however, this effect was weaker for forbs than for grasses, and became less pronounced with time (Fig. 1E and 1F). Forb and grass stem density changed with time (Table S4) and were generally lower in earlier years (2015 and 2016) than in later years (2017 and 2018; Fig. 1B, 1C, 1E, and 1F).

Cover

Cover of native plants, annual weeds, perennial weeds, and bare ground differed between seed mixes (Table S5; term for perennial weeds was marginally significant, $p = 0.096$). Native plant cover was consistently higher in the Economy and Diversity mixes than in the Pollinator mix (Fig. 2A), annual weed cover was higher in the Pollinator mix than in the Economy and Diversity mixes in 2017 (Fig. 2B), perennial weed cover was higher in the Pollinator mix than in the Economy and Diversity mixes in 2017 and 2018 (Fig. 2C), and bare ground cover was higher in the Pollinator mix than in the Economy and Diversity mixes every year (Fig. 2D). First year management influenced cover of native plants and annual weeds, but this effect became less pronounced with time (Table S5). More specifically, native plant cover was higher and annual weed cover was lower in mowed plots than in plots that were not mowed in 2016, but this effect was no longer significant in 2017 and 2018 (Fig. 2E and 2F). In general, cover of native plants and perennial weeds increased with time, while cover of annual weeds and bare ground decreased with time (Table S5; Fig. 2A–H).

Inflorescence Production and Floral Richness

Cumulative inflorescence production over the 3 years (2016–2018) differed between seed mixes (Table S6). The Pollinator mix produced more inflorescences than the Diversity mix and the Diversity mix produced more inflorescences

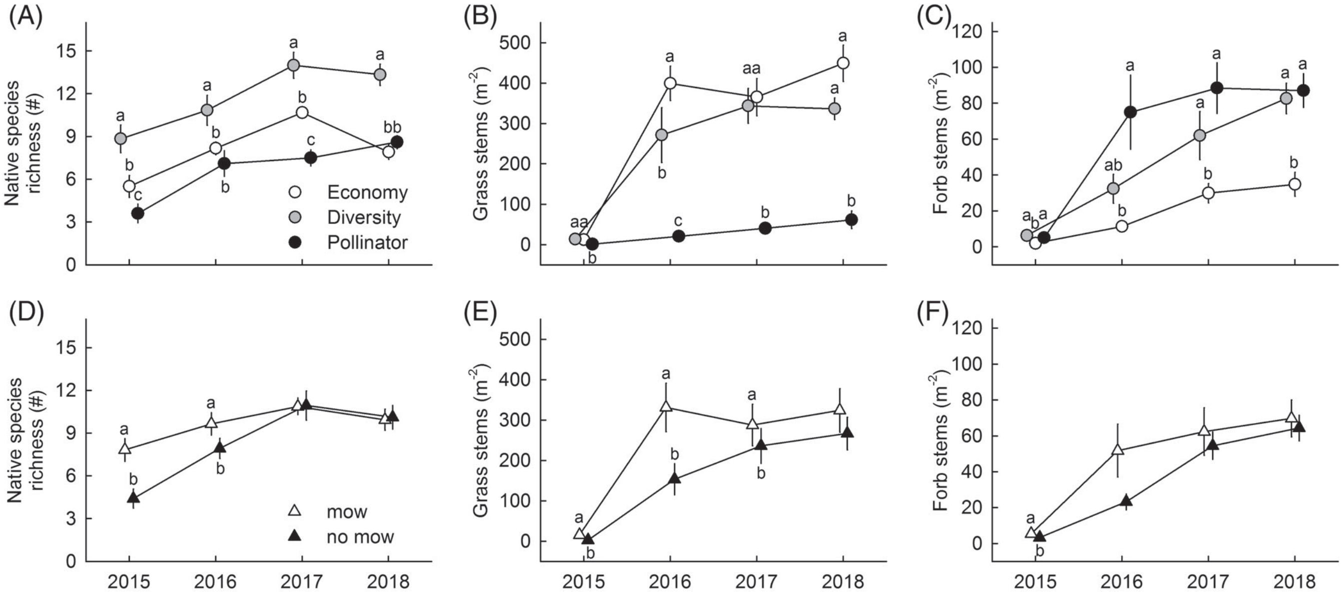

Figure 1. Differences in native species richness, native grass stem density, and native forb stem density between seed mixes (A–C) and mowing treatments (D–F). Values presented are annual averages (± 1 SE). Significant differences between seed mixes and mowing treatments (within a given year) based on Tukey's post hoc tests are indicated with different lowercase letters.

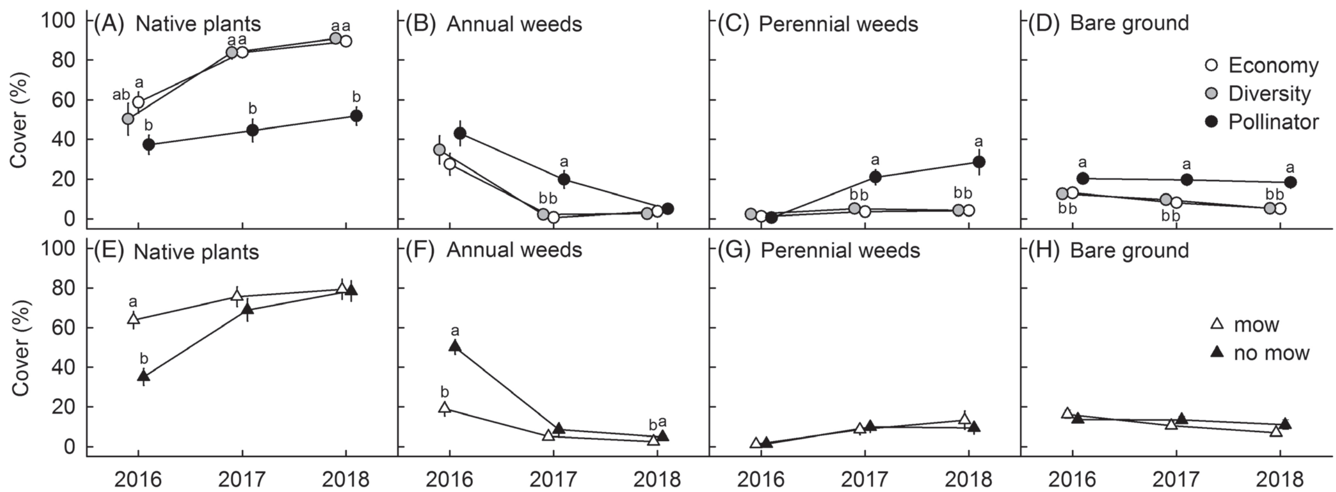

Figure 2. Differences in percent cover by native plants, annual weeds, perennial weeds, and bare ground between seed mixes (A–D) and mowing treatments (E–H). Values presented are annual averages (± 1 SE). Significant differences between seed mixes and mowing treatments (within a given year) based on Tukey's post hoc tests are indicated with different lowercase letters.

than the Economy mix (Fig. 3). First year management affected inflorescence production, but the effect of this treatment differed between seed mixes (Table S6). In particular, mowing increased inflorescence production in the Pollinator and Diversity mixes but decreased inflorescence production in the Economy mix (Fig. 3).

In total, seven planted forb species flowered in the Economy mix, 13 planted forb species flowered in the Pollinator mix, and 16 planted forb species flowered in the Diversity mix (Table 1). Species accounting for a high percentage of total inflorescence production include: *Ratibida pinnata* (47.85%) and *Heliopsis helianthoides* (37.83%) in the Economy mix; *R. pinnata* (50.71%) and *Rudbeckia hirta* (36.14%) in the Pollinator mix; and *R. pinnata* (30.62%), *H. helianthoides* (20.01%), *R. hirta* (14.70%), and *Desmodium canadense* (9.85%) in the Diversity mix (Fig. 4 and Table 1).

Cost-Effectiveness

Seed mix design and mowing both influenced cost-effectiveness. The cost of producing 1,000 native stems differed between seed mixes ($p < 0.0001$, Table S6); specifically, the Economy mix was the most cost-effective seed mix and the Pollinator mix was the least cost-effective seed mix for

Table 1. A comparison of floral richness and floral evenness (i.e. the relative percentage of total inflorescence production by species) between seed mixes. Values represent the percentage of total inflorescence production (2016–2018) for each species within a given seed mix. Species are listed based on relative rank within each seed mix. The total number of inflorescences produced was 1,848 in the Economy mix, 3,929 in the Diversity mix, and 6,873 in the Pollinator mix.

Economy Mix		*Diversity Mix*		*Pollinator Mix*	
Ratibida pinnata	47.85%	*Ratibida pinnata*	30.62%	*Ratibida pinnata*	50.71%
Heliopsis helianthoides	37.83%	*Heliopsis helianthoides*	20.01%	*Rudbeckia hirta*	36.14%
Rudbeckia hirta	8.69%	*Rudbeckia hirta*	14.70%	*Zizia aurea*	6.05%
Solidago speciosa	2.25%	*Desmodium canadense*	9.85%	*Echinacea pallida*	2.47%
Zizia aurea	1.82%	*Symphyotrichum laeve*	7.14%	*Oligoneuron rigidum*	1.68%
Monarda fistulosa	1.47%	*Oligoneuron rigidum*	3.62%	*Monarda fistulosa*	1.22%
Astragalus canadensis	0.09%	*Desmanthus illinoensis*	3.60%	*Vernonia fasciculata*	0.74%
		Silphium integrifolium	2.52%	*Helenium autumnale*	0.40%
		Helianthus grosseserratus	2.28%	*Symphyotrichum laeve*	0.19%
		Zizia aurea	1.38%	*Desmodium canadense*	0.19%
		Astragalus canadensis	1.26%	*Solidago speciosa*	0.09%
		Monarda fistulosa	1.18%	*Eryngium yuccifolium*	0.07%
		Chamaecrista fasciculata	0.97%	*Astragalus canadensis*	0.05%
		Echinacea pallida	0.49%		
		Euthamia graminifolia	0.24%		
		Anemone cylindrica	0.12%		

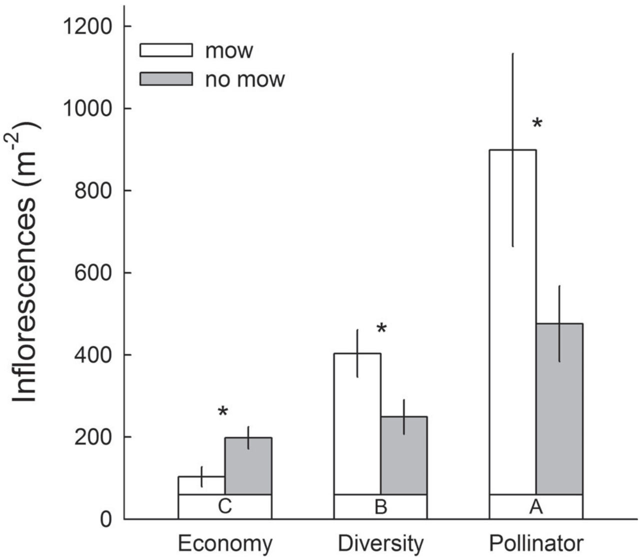

Figure 3. Differences in cumulative inflorescence production (2016–2018) between seed mixes and mowing treatments. Values presented are the average cumulative inflorescence production (± 1 SE) in a given treatment combination. Significant differences between seed mixes based on Tukey's post hoc tests are indicated by different letters on the bottom of the bars and significant differences between mowing treatments (within a given seed mix) based on Tukey's post hoc tests are indicated with asterisks.

producing stems (Table 2). On the other hand, the cost of producing inflorescences was 21% lower in the Pollinator mix than in the Economy mix (Table 2); however, this difference was not significant due to high variability in the Pollinator mix. The cost of producing 1,000 inflorescences differed between mowing treatments, but the effect of mowing on cost-effectiveness differed between seed mixes ($p = 0.0003$, Table S6). In particular, mowing increased cost-effectiveness in the Diversity and Pollinator mixes but decreased cost-effectiveness in the Economy mix (Table 2).

Discussion

In this study, we examine how seed mix design and first year management influence three ecosystem services commonly provided by tallgrass prairie reconstructions (erosion control, weed resistance, and pollinator resources). Consistent with previous studies (Larson et al. 2011, 2017; Grman et al. 2013; Phillips-Mao et al. 2015), our results show that seed mix design has a profound impact on ecological outcomes in prairie reconstruction. Our three seed mixes differed greatly in native stem density and native cover, which should influence a reconstruction's ability to provide erosion control (Boyd 1942; Ellison 1950; Durán Zuazo & Rodríguez Pleguezuelo 2008) and weed resistance (Schramm 1990; Bergelson et al. 1993; Stevenson et al. 1995; Van der Putten et al. 2000; Warren et al. 2002; Lepŝ et al. 2007; Török et al. 2010; Valkó et al. 2016). The three seed mixes also differed in inflorescence production and floral richness, which should influence a reconstruction's value as pollinator habitat (Hopwood 2008; Pywell et al. 2011). In agreement with other studies (e.g. Maron & Jefferies 2001; Antonsen & Olsson 2005), our results also show that management influences ecological outcomes in prairie reconstruction. First year mowing accelerated native plant establishment and inflorescence production, which should enhance ecosystem service provision during the early stages of a reconstruction.

Our results suggest that grass-dominated (Economy mix) and grass:forb balanced (Diversity mix) seed mixes provide better erosion control than commercially available forb-dominated mixes (Pollinator mix). Native stem density and native cover are two key determinants of erosion resistance (Boyd 1942; Ellison 1950; Durán Zuazo & Rodríguez Pleguezuelo 2008) and both were higher in the Economy and Diversity mixes than in the

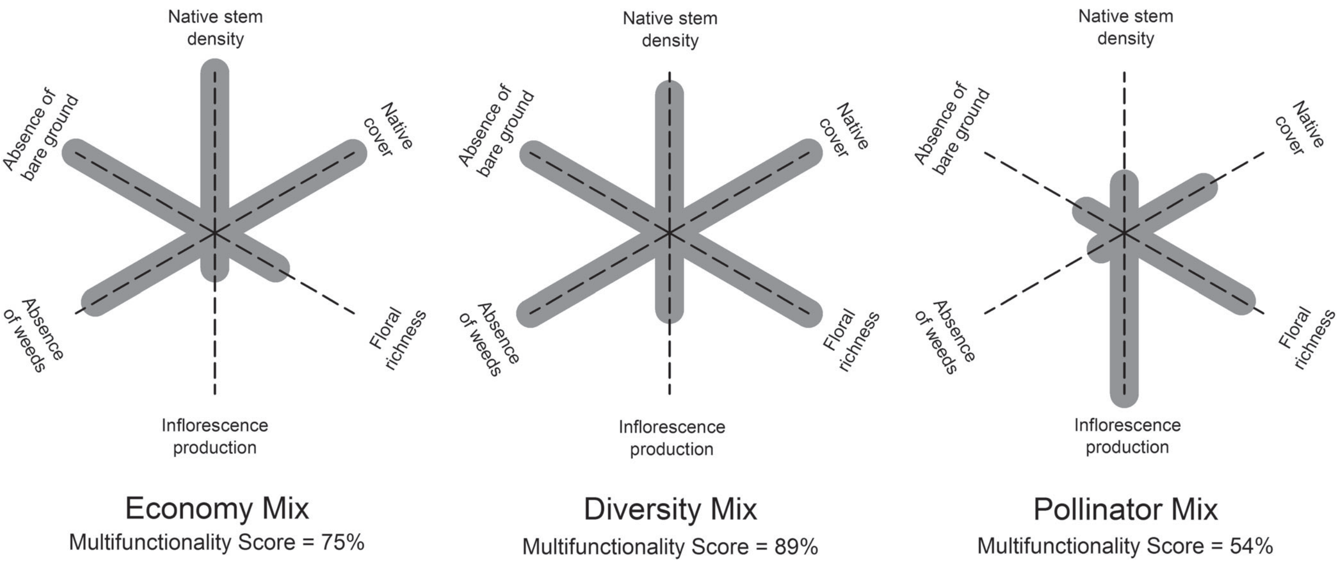

Figure 4. "Multifunctionality flowers" depicting the relative abilities of each seed mix to provide ecosystem services. Ability to provide erosion control was assessed using native cover (in 2018) and native stem density (in 2018). Ability to provide weed resistance was assessed using weed cover^{-1} (in 2018) and bare ground cover^{-1} (in 2018). Ability to provide pollinator resources was assessed using inflorescence production (total inflorescences produced, 2016–2018) and floral richness (total species that produced inflorescences, 2016–2018). The seed mix with the highest value for each variable was scored as a 1.0 and other seed mixes were scored as a relative proportion of that total. For clarity, we present each seed mix's multifunctionality score as a percentage out of 100.

Table 2. Assessing the influence of seed mix design and first year management on cost-effectiveness in prairie reconstruction. Cost-effectiveness was determined as the cost of the seed mix per plot divided by either: (1) the number of 1K native stems in 2018 or (2) the number of 1K inflorescences produced between 2016 and 2018, per plot. To improve normality and homoscedasticity of residual variation, the cost of producing 1,000 native stems was 1/square root-transformed. Significant differences between seed mixes (within a given mowing treatment) based on Tukey's post hoc tests are indicated with different letters. There were no significant differences between mowing treatments (within a given seed mix) based on Tukey's post hoc tests.

	Economy Mix	*Diversity Mix*	*Pollinator Mix*
1K native stems			
Mow	$0.06 (0.00)a	$0.15 (0.01)b	$0.56 (0.10)b
No mow	$0.07 (0.01)	$0.15 (0.02)	$0.51 (0.16)
1K inflorescences			
Mow	$0.39 (0.07)	$0.20 (0.02)	$0.13 (0.03)
No mow	$0.18 (0.03)	$0.33 (0.05)	$0.23 (0.05)

Pollinator mix. Differences in stem density and cover between the Economy and Pollinator mixes were likely related to their respective grass-to-forb seeding ratios. Grasses have higher germination rates than most forbs and also tend to fill in canopy gaps in prairie reconstructions. These attributes align well with several goals of USDA's Rare and Declining Habitat Conservation Practice (CP25), such as providing cover for wildlife and erosion control (United States Department of Agriculture 2015). The Pollinator mix, conversely, was designed to resemble a seed mix that met the specifications for USDA's Pollinator Habitat Conservation Practice (CP42). Grasses are seeded at a low rate in CP42 seed mixes to reduce competition for native forbs; however, previous studies have suggested that low grass seeding rates increase bare ground in prairie reconstructions (Dickson & Busby 2009) and our results support that conclusion. Despite having a balanced grass-to-forb seeding ratio, the Diversity mix produced stands with comparable native stem density and cover to the Economy mix. This suggests that prairie reconstructions can achieve the same degree of erosion control at a lower grass-to-forb seeding ratio with a seed mix customized to site soil conditions.

Our results suggest that grass-dominated (Economy mix) and grass:forb balanced (Diversity mix) seed mixes are also more resistant to weed invasion than forb-dominated seed mixes (Pollinator mix). Prairie reconstructions with low rates of native establishment tend to be more susceptible to weed invasion (Middleton et al. 2010; Carter & Blair 2012; Nemec et al. 2013). The Pollinator mix had more bare ground than the Economy and Diversity mixes, which likely contributed to its higher invasibility. Perennial weed cover also increased with time in the Pollinator mix and by year 4 (2018), represented approximately 25% of total cover. This result is particularly concerning as perennial weeds can reduce native richness and diversity (Blumenthal et al. 2003; Martin & Wilsey 2012) and increase long-term management costs in prairie reconstructions. By comparison, perennial weeds consistently accounted for less than 5% of the total cover in the Economy and Diversity mixes.

Our results suggest that forb-dominated (Pollinator mix) and grass:forb balanced (Diversity mix) seed mixes provide higher quality habitat for pollinators than grass-dominated seed mixes (Economy mix). Floral abundance is a key determinant of pollinator habitat quality (Hopwood 2008; Pywell et al. 2011). We found that the Pollinator mix produced the highest number of inflorescences, while the Economy mix produced the lowest number of inflorescences. Another determinant of pollinator habitat quality is floral richness (Hopwood 2008; Pywell et al. 2011). Highlighting the importance of floral richness for pollinator-habitat quality, to meet the requirements of CP42, a seed mix must contain a minimum of three flowering species from each of three different bloom periods throughout the growing season (United States Department of Agriculture 2011). Floral richness was higher in the Diversity mix (16 flowering forb species) than in the Pollinator (13 flowering forb species) and Economy (7 flowering forb species) mixes. Also, the Diversity and Pollinator mixes provided floral resources throughout the growing season (spring, summer, and fall) while the Economy mix only provided floral resources in spring and summer. The Diversity mix also had higher floral evenness than the other two mixes. Pielou's evenness index for inflorescence production in the Diversity mix ($J' = 0.74$) was 60% higher than in the Pollinator mix ($J' = 0.47$) and 25% higher than in the Economy mix ($J' = 0.60$). Two species accounted for more than 85% of all inflorescence production in both the Pollinator (*Ratibida pinnata* and *Rudbeckia hirta*) and Economy (*R. pinnata* and *Heliopsis helianthoides*) mixes. Because *R. hirta* in particular is an early successional species that fades over time (Williams et al. 2007), floral resources in these mixes may be expected to decline over time as well. Conversely, in the Diversity mix, the top two species only accounted for 50% of all inflorescence production and eight species produced at least 100 surveyed inflorescences throughout the study period. Previous research has shown that floral evenness enhances facilitative pollinator attraction in some plant species (Ghazoul 2006). Further, although we could not compare floral diversity between seed mixes in our study because of difference in seeded forb diversity, a reduction in floral evenness would concurrently lead to a reduction in floral diversity, and previous studies have shown that floral diversity and pollinator diversity are correlated in tallgrass prairies (e.g. Hines & Hendrix 2005; Hopwood 2008; Myers et al. 2012).

Multifunctionality (i.e. the ability to concurrently provide erosion control, weed resistance, and pollinator resources) was highest in the Diversity mix (multifunctionality score = 89%), followed by the Economy (multifunctionality score = 75%) and Pollinator (multifunctionality score = 54%) mixes. Our results suggest that the Economy mix would effectively provide erosion control and weed resistance, but not pollinator resources. Our results suggest that the Pollinator mix would effectively provide pollinator resources, but not erosion control or weed resistance. Our results also suggest that the Diversity mix would effectively provide all three ecosystem services. Further, a multifunctionality score of 89% suggests that the Diversity mix would provide erosion control and pollinator resources in a comparable manner to seed mixes designed to achieve these specific ecological outcomes. As such, seed mixes like the Diversity mix (i.e. a site-customized, high-diversity, grass:forb balanced seed mix) would be a good option for land managers that want to enhance pollinator resources on the landscape but have been dissuaded by the potential for weeds or high seed costs of commercially available forb-dominated mixes. Similarly, it would be a good option for land managers that need the services of grass-dominated stands (e.g. filtering nutrient run-off, erosion control, weed resistance) but want a seed mix that provides better pollinator resources.

Our results show that first year mowing accelerates native plant establishment and inflorescence production in prairie reconstructions. In the early years of this study, mowed plots had higher species richness, higher native grass and forb stem density, higher native plant cover, and lower annual weed cover than plots that were not mowed. Positive effects in these initial years can have longer-lasting impacts on community establishment. Priority effects (i.e. the order in which species arrive and establish) play an important role in shaping reconstructed prairie communities (Temperton & Hobbs 2004). Previous studies have shown that non-native species outcompete native grassland species when they arrive and establish first (Dickson et al. 2012; Wilsey et al. 2015). In addition to native establishment, mowing increased inflorescence production in the Pollinator and Diversity mixes. An enhancement of pollinator resources during establishment years would increase the lifetime value of prairie reconstructions as pollinator habitat. Interestingly, mowing decreased inflorescence production in the Economy mix, suggesting that mowing may have benefited the most abundant planted species (grasses) at the expense of those less abundant (forbs). Over time, this trend may further reduce the pollinator habitat value of grass-dominated seed mixes. In this study, we restricted mowing to the first growing season because of a previous study which found that second year mowing does not generally improve the establishment of forbs sown into warm-season prairie grass stands (Williams et al. 2007). Nevertheless, future research could examine whether prolonged mowing improves establishment in any hard-to-establish forbs, as some species (e.g., *Solidago rigida*) did respond positively to second year mowing in the Williams et al. (2007) study.

Cost-effectiveness has been a long-standing concern of the CRP (United States General Accounting Office 1992). While it can be difficult to link the dollar value of a program to its environmental benefit, we attempted to assess cost-effectiveness in these seed mixes by relating the cost of each seed mix to the ecosystem services it provided (native stem density for erosion control and inflorescence production for pollinator resources). The Economy mix (seed cost = $321/ha) was the most cost-effective seed mix for producing stems, but the least cost-effective seed mix for producing inflorescences, particularly in mowed plots. The Pollinator mix ($909/ha), on average, was the most cost-effective seed mix for producing inflorescences, but the least cost-effective seed mix for producing stems. The Diversity mix ($719/ha) had comparable (but slightly lower) cost-effectiveness to the Economy mix for producing stems and comparable (but slightly lower) cost-effectiveness to the Pollinator mix for producing inflorescences. This suggests that a site-customized, high-diversity, grass:forb balanced seed mix achieves high multifunctionality in a cost-effective manner. Future research in our lab will replicate this experiment at a new site under different planting conditions that have been shown to influence individual species establishment (e.g. season of planting, see Peters & Schottler

2010). This study will help us identify and adjust seeding rates for species with consistently poor establishment from the Diversity mix and further improve the cost-effectiveness of this seed mix.

Because resources such as funding and acreage for conservation are finite, programs must consider the efficiency with which they address specific conservation concerns. While many of the CPs designed to enhance single ecosystem services have proven effective, some of these practices could be more multifunctional. In this study, we show that a site-customized, high-diversity, grass:forb balanced seed mix can produce a prairie reconstruction that is both multifunctional (i.e. provides erosion control, weed resistance, and pollinator resources) and cost-effective. Although the Diversity mix would meet the necessary criteria of several CPs, including CP25, cost-share for seed is typically extremely limited under these CPs. Ultimately, our research highlights the need to create a new CP (or to update an existing CP) focused on whole ecosystem restoration of native tallgrass prairie.

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Supporting Information

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

Figure S1. Plot layout of the research site.
Table S1. Seed mix and seeding rate of the Economy mix.
Table S2. Seed mix and seeding rate of the Pollinator mix.
Table S3. Seed mix and seeding rate of the Diversity mix.
Table S4. Repeated measures ANOVA table: species richness, grass stem density, and forb stem density.
Table S5. Repeated measures ANOVA table: percent cover by native plants, annual weeds, perennial weeds, and bare ground.
Table S6. Two-way ANOVA table: cumulative inflorescence production and cost-effectiveness.

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