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RESEARCH ARTICLE

Planting time, first-year mowing, and seed mix design influence ecological outcomes in agroecosystem revegetation projects

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The conversion of tallgrass prairie to agriculture has negatively affected provisioning of ecosystem services. Successful restoration of ecosystem services could depend on management decisions applied during revegetation projects. We examined the effects of three management decisions (seed mix design, planting time, and first-year mowing) on targeted ecosystem services (erosion control, weed resistance, and pollinator resources). We tested three seed mixes of varying diversity and grass-to-forb seeding ratios: Economy mix (21 species, 3:1 grass:forb), Pollinator mix (38 species, 1:3), and Diversity mix (71 species, 1:1). We established plots at two planting times (dormant-season and spring) with or without first-year mowing. To assess ecosystem services, we measured stem density, canopy cover, and floral density and richness of sown species in the second year after planting. The Economy mix had the highest stem density and cover but lowest floral density and richness. The Pollinator mix had the lowest stem density and cover but highest floral density. The Diversity mix had comparable stem density and cover to the Economy mix and comparable floral density and richness to the Pollinator mix. Mowing accelerated native plant establishment in all seed mixes. Dormant-season planting improved establishment of spring and fall forbs and favored cool-season graminoids over warm-season grasses. All three management decisions influenced ecosystem outcomes, and comparison to a previous study revealed these effects to be robust to variation in site and climatic conditions. We recommend a diverse, balanced seed mix design, first-year mowing, and dormant-season planting to improve multifunctionality of conservation projects.

Key words: ecosystem services, erosion control, pollinator habitat, revegetation projects, tallgrass prairie, weed resistance

Implications for Practice

- Seed mix design is a strong determinant of ecological outcomes, and a diverse, grass-to-forb balanced seed mix can enhance multiple ecosystem services in the agricultural landscape.
- By mowing frequently during the first year of establishment, ecosystem services can accrue more quickly in agroecosystem revegetation projects.
- Dormant-season planting is a no-cost strategy that may improve the provisioning of pollinator resources by favoring establishment of spring and fall forbs and reducing establishment of competitive warm-season grasses.
- Improving early establishment outcomes using best management practices identified in this study can substantially increase lifetime ecosystem service provision in short-lived agroecosystem revegetation projects.

Introduction

The conversion of tallgrass prairie to agriculture in the Midwestern United States and the subsequent intensification of agricultural production in the region has resulted in extensive habitat degradation and negatively affected the provisioning of ecosystem services (e.g., water quality protection, flood control, carbon sequestration, wildlife habitat, pollinator habitat) (Wright & Wimberly 2013). To restore these ecosystem services to the agricultural landscape, various state and federal agencies and conservation organizations have developed targeted programs to address specific conservation challenges. With over 20 million acres (8 million hectares) currently enrolled, the United States Department of Agriculture's (USDA) Conservation Reserve Program (CRP) is a globally significant, large-scale conservation initiative. This program provides landowners with cost-share and/or rental payments to temporarily retire environmentally sensitive lands from agricultural production and

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implement a conservation practice involving revegetation. Two prominent CRP conservation practices in the Midwestern United States are CP25, which is designed to reduce soil erosion and provide habitat for declining wildlife species, and CP42, which is designed to enhance pollinator habitat (USDA 2021). To ensure that conservation initiatives produce their intended ecosystem services at a high-level and in a consistent manner, we need to better understand how management decisions influence ecological outcomes in revegetation projects (e.g., Larson et al. 2011, 2017; Grman et al. 2013). Seed mix design, the seasonal timing of planting, and first-year mowing are three management variables likely to affect outcomes in grassland revegetation projects.

Seed mix design is one of the most significant determinants of ecological outcomes in revegetation projects involving native grass and forb species (Grman et al. 2013). A key aspect of seed mix design is the grass-to-forb seeding ratio. Seed mixes with high grass-to-forb seeding ratios typically produce dense, grass-dominated stands. These stands are well suited for conservation projects striving to prevent soil erosion, minimize nutrient loss, and enhance water quality but poorly suited for projects striving to enhance pollinator habitat. Forbs establish poorly and often do not persist in grass-dominated stands (Dickson & Busby 2009; McCain et al. 2010; Török et al. 2010). Conversely, seed mixes with low grass-to-forb seeding ratios typically produce higher quality pollinator habitat than grass-dominated stands but are also less dense, more prone to weed invasion (Middleton et al. 2010; Carter & Blair 2012; Nemec et al. 2013), and provide less protection against soil erosion and water quality degradation (Boyd 1942; Ellison 1950; Burke & Grime 1996). Seed mixes with balanced (1:1) grass-to-forb seeding ratios have the potential to be more multifunctional, providing erosion control and weed resistance comparable to grass-dominated seed mixes and pollinator habitat quality comparable to forb-dominated seed mixes (Meissen et al. 2020).

The seasonal timing of planting is another management decision that could influence outcomes in conservation projects. Most revegetation projects in the Midwestern United States involve planting in spring or in late fall when the vegetation is dormant, and many CRP contracts are implemented with spring planting because of various logistical obstacles involved in management (e.g., weather, seed availability, equipment availability). However, dormant-season planting may be ecologically preferable to spring planting because it allows seeds to experience freeze–thaw cycles, increases seed to soil contact, and better mimics natural stratification and germination conditions (Rowe 2010), resulting in higher forb establishment compared to spring planting, which favors C_4-grass establishment (Larson et al. 2011). Forb establishment rates are typically low in prairie restoration projects (Smith et al. 2010; Williams et al. 2010) and many species require specific environmental cues to germinate successfully (Chambers & MacMahon 1994). Species that fail to germinate in their first growing season are susceptible to predation and fungal attacks until they receive the proper germination cue (Clark & Wilson 2003). This may explain why approximately one third of species fail to establish in CRP conservation projects (Hillhouse & Zedler 2011). Many of the forb species commonly used in native prairie revegetation projects have seed that is expensive to produce (Smith et al. 2010), and seeds that fail to recruit as plants contribute to poor cost-effectiveness. Dormant-season planting could be a no-cost strategy for improving forb establishment in conservation projects.

First-year mowing is another management decision that could influence outcomes in conservation projects. Fast-growing annual weeds are a common problem in revegetation projects implemented on high-nutrient, post-agricultural lands (Rothrock & Squiers 2003). Annual weeds can quickly form a dense canopy and restrict light to developing native seedlings. First-year mowing increases light availability and reduces competition for native seedlings (Copeland et al. 2002; MacDougall & Turkington 2007; Williams et al. 2007), which can promote forb establishment (Williams et al. 2007; Rowe 2010), increase native species richness (Meissen et al. 2020), increase floral resources (Endels et al. 2007; Meissen et al. 2020) and reduce invasion (Smith et al. 2018). Nevertheless, a survey of 38 experts revealed that only 60–65% of practitioners mow during the early years of a tallgrass prairie restoration (Rowe 2010). Because CRP contracts typically last only 10–15 years, it is imperative that native plants establish quickly to realize the maximum ecological benefits over the lifetime of the contract. If mowing accelerates or improves forb establishment, then it could significantly increase the lifetime ecosystem service provision of a CRP contract at a relatively low cost (Phillips-Mao et al. 2015).

Site conditions, annual rainfall, and landscape factors can all influence outcomes in restoration projects (Bakker et al. 2003; MacDougall et al. 2008; Matthews et al. 2009, 2017); however, very few restoration studies are replicated at different sites or in different years (Sutherland et al. 2004; Rowe 2010; Fraser et al. 2020). In a previous study performed at a different research site (Meissen et al. 2020), we demonstrated that seed mix design and first-year mowing influence ecological outcomes in conservation projects; however, the effects of planting time were not assessed. In this study, we replicated the experimental design of Meissen et al. (2020) at a new site and added one additional management decision: the effects of dormant-season versus spring planting. We established research plots using a full factorial design: three seed mixes with different diversity and grass-to-forb seeding ratios (3:1, 1:1, and 1:3), two planting times (dormant season and spring), and two first-year mowing treatments (mown and unmown). To assess ecological outcomes, we measured sown species richness, stem density (sown grasses and sown forbs), cover (sown plants, unsown native plants, annual weeds, perennial weeds, and bare ground), sown floral density, and sown floral richness in the second year after establishment. To assess whether the effects of seed mix design and first-year mowing are robust to site, annual, and landscape variability, we compared the results of the current study to Meissen et al. (2020). The consistency with which management decisions impact ecological outcomes will influence the likelihood of widespread implementation by restoration practitioners.

Methods

Study Site

We conducted this study at the University of Northern Iowa's Tallgrass Prairie Center in Cedar Falls, Iowa, USA (42°30′N, 92°28′W). The land used to establish this research site had previously been used for corn and soybean production, with corn produced the year prior to retirement. The site is relatively level (slopes not exceeding a 5% grade) and the soil is a mixture of Clyde-Floyd complex (approximately 90%) and Kenyon loam (approximately 10%) (Natural Resources Conservation Service 2021).

Seed Mixes and Seeding Rate

We established research plots with three different seed mixes, which we named the Economy mix, Diversity mix, and Pollinator mix. We designed the seed mixes to meet the seed mix criteria of three CRP conservation practices. The seed mixes differed in grass-to-forb seeding ratios, diversity, and species composition.

We designed the Economy mix to meet the seed mix criteria of CP25: Rare and Declining Habitat. This conservation practice strives to reduce soil erosion and provide habitat for declining wildlife species. CP25 stands typically have low to moderate diversity and are planted with a higher density of grass seed than forb seed. Accordingly, our Economy mix consisted of 21 native grass and forb species at a 3:1 grass-to-forb seeding ratio (Table S1). The cost of the Economy mix was \$85 ha^{-1}.

We designed the Diversity mix to meet the seed mix criteria of CP43: Prairie Strips. CP43 was established in the 2018 Farm Bill and is growing in popularity in the Midwestern United States. This conservation practice strives to reduce nutrient loss, improve water quality, reduce soil erosion, and provide wildlife habitat. The USDA recommends that CP43 stands be planted with a diverse, balanced mixture of grass and forb seed. Accordingly, our Diversity mix consisted of 71 native species at a 1:1 grass-to-forb seeding ratio (Table S2). The cost of the Diversity mix was \$218 ha^{-1}.

We designed the Pollinator mix to meet the seed mix criteria of CP42: Pollinator Habitat. This conservation practice strives to enhance pollinator abundance by providing at least three flowering species in bloom during spring, summer, and fall. CP42 stands are planted with a higher density of forb seed than grass seed. Accordingly, our Pollinator mix consisted of 38 native species at a 1:3 grass-to-forb seeding ratio (Table S3). The cost of the Pollinator mix was \$327 ha^{-1}.

We purchased seed from native seed nurseries in Iowa in 2018 and stored it in coolers at 4°C and 45% relative humidity prior to sowing. We weighed, bagged, and mixed the seed for each plot separately. We used a seeding rate of 430 pure live seed/m^2.

Seasonal Planting Time

We established plots with two different planting times: dormant-season and spring. We performed the dormant-season planting in November 2018 and the spring planting in April 2019 after the ground had thawed. We used a Truax FLX-86U no-till drill for both planting time treatments. Prior to planting, we prepared the soil by performing four passes with a disk cultivator to break up residual corn litter and one harrow pass to create a uniform soil surface.

First-Year Mowing

We established research plots with two different first-year mowing treatments: mown and unmown. Plots that received the mowing treatment (mown plots) were mowed with a Toro 2000 Titan HD to a height of approximately 13 cm four times during the 2019 growing season: 12 June, 11 July, 8 August, and 28 October. Plots that did not receive the mowing treatment (unmown plots) were not mowed in 2019; however, in unmown plots, we clipped plants that were within 0.5 m of the plot edge to a height of 1 m in November 2019 to prevent tall vegetation (>3 m) from falling over or dispersing seed into adjacent plots. We left all thatch on site in both mown and unmown plots.

Experimental Design. We established 72 rectangular research plots (8.5 m × 6.1 m each) using a randomized split-plot design. The 72 research plots were divided into two spatial blocks with each block containing 18 split plots (8.5 m × 12.2 m each). The 18 split plots were randomly assigned three replicates of each seed mix × planting time treatment combination. In each split-plot, we randomly selected one half as the mown subplot and the other half as the unmown subplot (i.e., the mowing treatment represented the subplot within the main plots which consisted of a seed mix × planting time treatment combination). Overall, our experimental design was: 3 seed mixes × 2 planting times × 2 first-year mowing treatments × 3 replicates × 2 spatial blocks = 72 research plots (Fig. 1).

Data Collection

We collected habitat data at the end of the second growing season (August 2020). We established a randomly positioned 5.5 m transect on the east–west axis of each plot. Along each transect, we recorded the number of ramets greater than 10 cm tall of all sown species in five 0.125-m quadrats. In the same quadrats, we also recorded cover (at observer height [1.2 m], to the nearest 5%) for the following classes: sown plants, unsown native perennials, perennial weeds, annual/biennial weeds, and bare ground. Unsown native perennials were defined as potentially desirable native species that were not part of the original seed mix (e.g., *Solidago altissima*, *Symphyotrichum pilosum*, *Geum* sp., and *Potentilla* sp.). The occurrence of these species was likely due to the adjacency of our experiment site to a naturalized hedgerow habitat, which is atypical of most post-agricultural prairie reconstructions. However, some species may have originated from seed mix contamination, dispersal from adjacent research plots, or regeneration from recently farmed land. We categorized undesirable native and non-native species as annual/biennial (e.g., *Ambrosia trifida*, *Conyza canadensis*) or perennial (e.g., *Poa pratensis*, *Taraxacum officinale*)

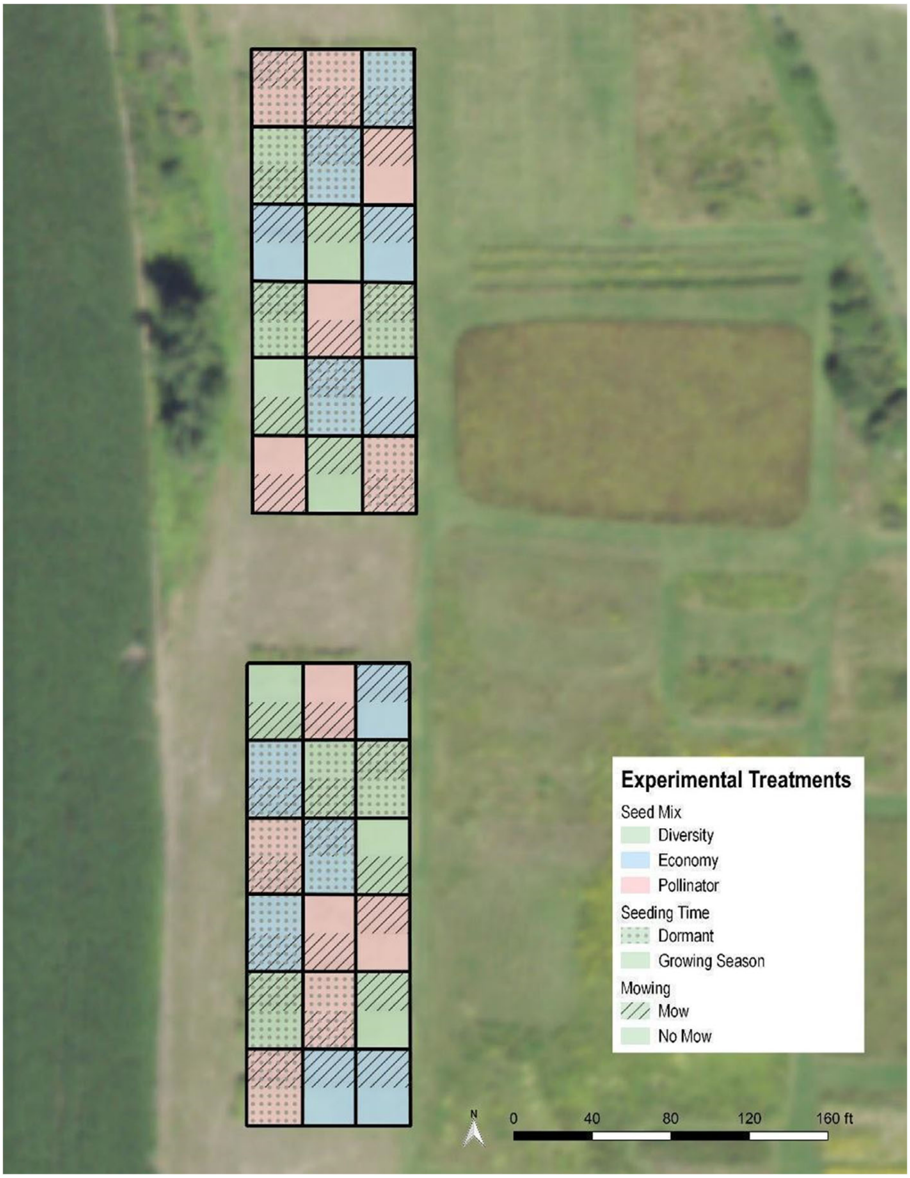

Figure 1. The field experiment at the Cedar Falls, Iowa site employed a randomized split-plot design with 72 research plots divided into two spatial blocks. Each block included 18 split plots, which were randomly assigned to one of six possible seed mix × planting time treatment combinations (three replicates of each per block). The mowing treatment represented the subplot and was applied randomly to half of each split plot.

weeds (for complete categorization of all unsown species, see Table S6). In addition to stem density of sown species and cover, we recorded the number of inflorescences and species of sown forbs rooted in the quadrat (sown floral density and richness). The timing of our survey coincided with the peak bloom period for these seed mixes; however, we acknowledge that we might have missed early-flowering species that had already senesced and species that had yet to flower with this approach. To minimize edge effects, we did not sample quadrats within 1 m of plot edges. In addition to the quadrat-sampling approach, we also performed a 5-minute meandering walk to record the presence/absence of sown species (sown species richness) and inflorescences (sown floral richness) in each plot. For the current study, we present data from the 5-minute meandering walk (number of species in plot) for sown species richness and floral richness in our results because this approach was more likely to capture rare species. However, for our cross-study comparison (see below), we present data on sown species richness and floral richness from the quadrat sampling (number of species/m^2) approach for the purpose of interstudy consistency.

Data Analysis

We compared response variables between treatment combinations using analysis of variance (ANOVA), with seed mix, planting time, and first-year mowing as fixed factors, and plot nested within block as a random factor. To meet the assumptions of normality and homoscedasticity of residual variance, sown graminoid stem density, sown forb stem density, sown inflorescence number, and perennial weed cover were cube-root transformed and sown floral richness, sown plant cover, unsown native plant cover, annual weed cover, sown species richness and sown floral richness were square-root transformed. We determined the optimal transformations using Box-Cox analyses. Post hoc comparisons of significant treatment effects were made using Tukey HSD tests.

To further examine the effect of planting time on community composition, we classified sown species into six functional groups: cool-season graminoids (grasses and sedges), warm-season grasses, spring forbs, summer forbs, legumes, or fall forbs (Tables S1–S3). We summed the stem density of all species in each functional group and tested for differences between planting times using ANOVA, with seed mix, planting time, and first-year mowing as fixed factors and plot nested within block as a random factor. To meet the assumptions of normality and homoscedasticity of residual variance, warm-season grasses, cool-season graminoids, all graminoids, summer forbs, fall forbs and all forbs were cube-root transformed, spring forbs were sqrt^{-1}-transformed, and legumes were 1/yr-transformed. We interpreted the main effect of planting time and plotted the means and standard errors of each functional group pooled across seed mixes and mowing treatments for comparison. ANOVAs, Tukey HSD tests, Box-Cox analyses, and transformations were performed in R (v. 3.6.1. R Core Team 2019).

Because of past research demonstrating differences in forb establishment by planting time (Larson et al. 2011) and the importance of successful forb establishment for projects aiming to create pollinator habitat, we examined differences in community composition between dormant-season and spring planted Pollinator mix plots. We square-root transformed the stem density data for sown species to reduce the influence of dominant species, generated a Bray–Curtis similarity matrix, and employed non-metric multidimensional scaling to visualize patterns of variation in community composition. We tested for differences in community composition using PERMANOVA with planting time and mowing treatment as fixed factors and block as a random factor (Anderson et al. 2008). We used similarity percentages analysis (SIMPER; Clarke & Gorley 2015) to identify species favored by dormant-season or spring planting. Within each functional group, we ranked species in decreasing order by their relative contribution to Bray–Curtis dissimilarity between dormant-season and spring planted plots. Community analyses were performed using PRIMER 6 (version 6.1.13) with PERMANOVA+ (version 1.0.3) (PRIMER-E Ltd., Plymouth, UK) software.

Cross-Site Comparison of Seed Mix Design and First-Year Mowing Effects

To examine whether the effects of seed mix design and first-year mowing are robust to site, annual, and landscape variability, we compared the results of the current study to a previous study (Meissen et al. 2020). The previous study was conducted from 2015 to 2019 at Iowa State Northeast Research and Demonstration Farm in Nashua, Iowa (42°56′N, 92°34′W). The Nashua site is relatively level (slopes not exceeding a 5% grade); the soil is primarily poorly drained Clyde clay loams with a minor component of somewhat poorly drained Floyd loams (Natural Resources Conservation Service 2021). The land used to establish the Nashua site had previously been used for corn and soybean production, with soybean produced the year prior to retirement. We refer to the site from the current study as "Cedar Falls" and the site from the previous study as "Nashua" throughout the manuscript.

The Nashua study used a similar experimental design to the Cedar Falls study (identical seed mixes, first-year mowing treatments, replication, and spatial blocking); however, there was no planting time treatment at Nashua; all plots at Nashua were spring planted. Therefore, the experimental design of the Nashua study was 3 seed mixes × 2 first-year mowing treatments × 3 replicates × 2 spatial blocks = 36 research plots (see fig. S1 in Meissen et al. 2020 for Nashua site map). Because of this difference in experimental design, we compared Nashua plots to spring planted Cedar Falls plots only.

We compared the effects of experimental treatment (i.e., seed mix and first-year mowing) on ecosystem service provision (erosion control, weed resistance, and pollinator resources) between the Nashua and Cedar Falls studies. To assess erosion control, we used sown cover and sown stem density, as these factors have previously been identified as key determinants of erosion resistance (Boyd 1942; Ellison 1950; Zuazo & Pleguezuelo 2009). To assess weed resistance, we used the absence of bare ground and the absence of weeds (Middleton et al. 2010; Carter & Blair 2012; Nemec et al. 2013). To assess pollinator resources, we used sown floral density and richness because these factors influence pollinator habitat quality (Ebeling et al. 2008; Hopwood 2008; Pywell et al. 2011). At each site, the seed mix with the highest value for each response variable was scored as 100% and the other two seed mixes were scored as the relative proportion of the highest value. We compared the mowing effect between studies using the same approach.

Results

Effects of Seed Mix, Planting Time, and Mowing

Sown Species Richness and Floral Richness. In general, all three management factors influenced species richness, and there was a significant seed mix × planting time interaction (Table S4). Species richness was highest in the Diversity mix and lowest in the Economy mix; higher in mown subplots than in unmown subplots; and higher with dormant-season planting than with spring planting (Fig. 2A). Planting time had stronger effects in the Diversity and Pollinator mixes than in the Economy mix (Fig. 2A).

Sown floral richness was highest in the Diversity mix and lowest in the Economy mix; higher in mown subplots than in unmown subplots; and higher with dormant-season planting than with spring planting (Fig. 2B). The significant seed

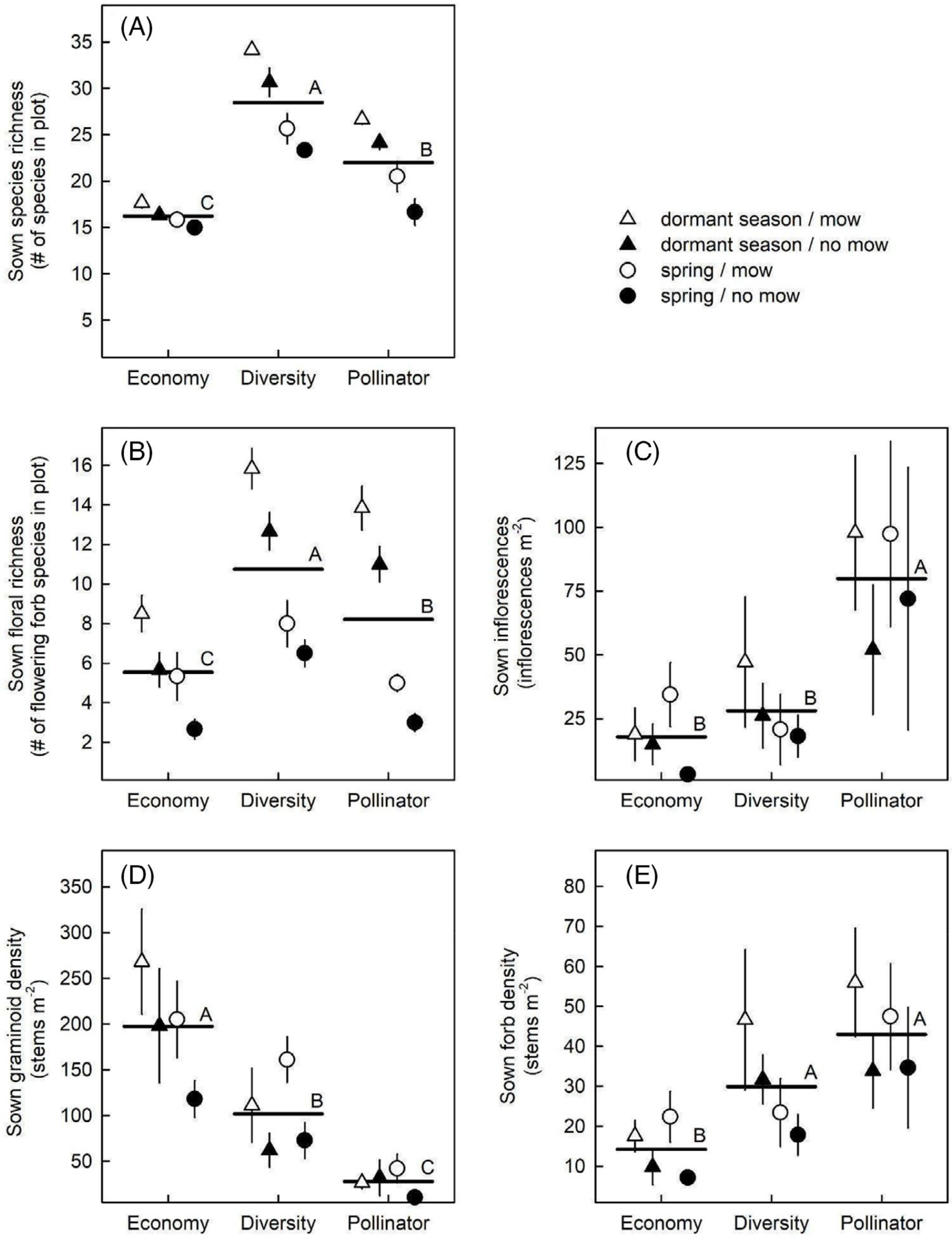

Figure 2. Mean (± SE) sown species richness (A), sown floral richness (B), sown inflorescences (C), sown graminoid density (D), and sown forb density (E) by seed mix and mowing/planting time treatment combinations. Significant differences between seed mixes based on Tukey's post hoc tests are indicated with capital letters.

mix × planting time interaction occurred because the Pollinator mix had higher floral richness than the Economy mix with dormant-season planting but not with spring planting (Fig. 2B).

Sown Floral, Graminoid, and Forb Densities. Generally, response variables affecting inflorescence or stem density were affected by seed mix and mowing treatment, but not planting time, and there were no significant interaction terms. (Table S4). The Pollinator mix produced more inflorescences than the Economy and Diversity mixes (Fig. 2C), and inflorescence production was higher in mown subplots than unmown subplots (Fig. 2C). The Economy mix had the highest graminoid stem density and the Pollinator mix had the lowest graminoid stem density (Fig. 2D). The Diversity and Pollinator mixes had significantly higher forb stem density than the Economy mix (Fig. 2E). Mown subplots had higher graminoid and forb stem density than unmown subplots (Fig. 2D & 2E).

Cover. In general, cover by sown plants and annual weeds were affected strongly by seed mix and mowing (Table S5). Sown plant cover was higher in the Economy mix than in the Pollinator mix and mown subplots had higher sown plant cover than unmown subplots (Fig. 3A). Annual weed cover was higher in the Diversity mix than in the Economy mix, and lower in mown subplots than unmown subplots (Fig. 3C). In addition, mowing reduced bare ground cover compared to unmown subplots (Fig. 3E).

Planting time affected perennial weed and bare ground cover and had a marginally significant effect on sown plant cover

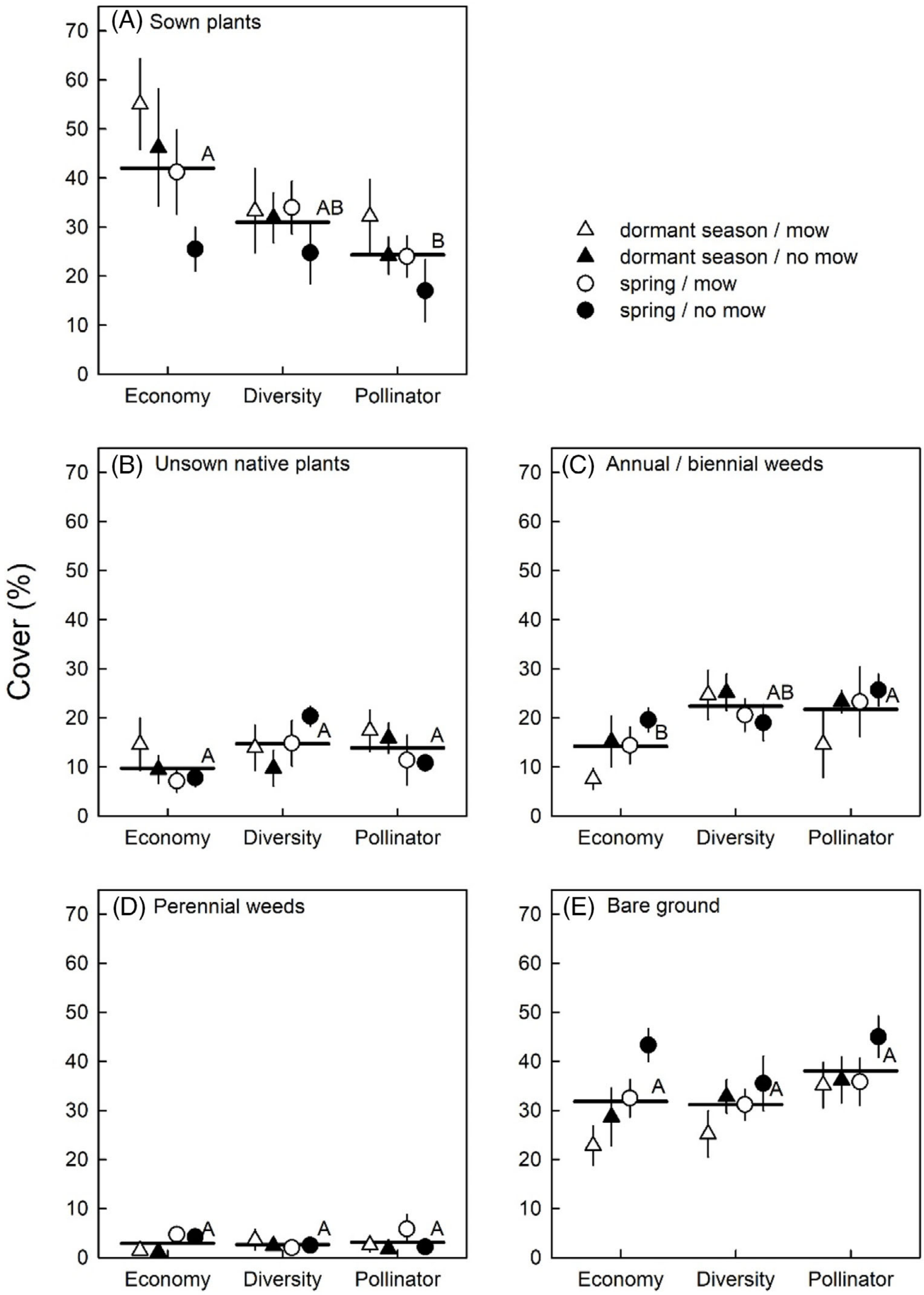

Figure 3. Mean (± SE) percent cover of sown plants (A), unsown native plants (B), annual (C) and perennial (D) weeds, and bare ground (E) by seed mix and mowing/planting time treatment combinations. We categorized desirable native species (e.g., *Solidago altissima*, *Symphyotrichum pilosum*, *Geum* spp., and *Potentilla* spp.) that were not part of the original seed mix but regenerated from the recently farmed land as unsown native plants. Conversely, we categorized undesirable native and non-native species as annual/biennial (e.g., *Ambrosia trifida*, *Conyza canadensis*) or perennial (e.g., *Poa pratensis*, *Taraxacum officinale*) weeds. Significant differences between seed mixes based on Tukey's post hoc tests are indicated with capital letters.

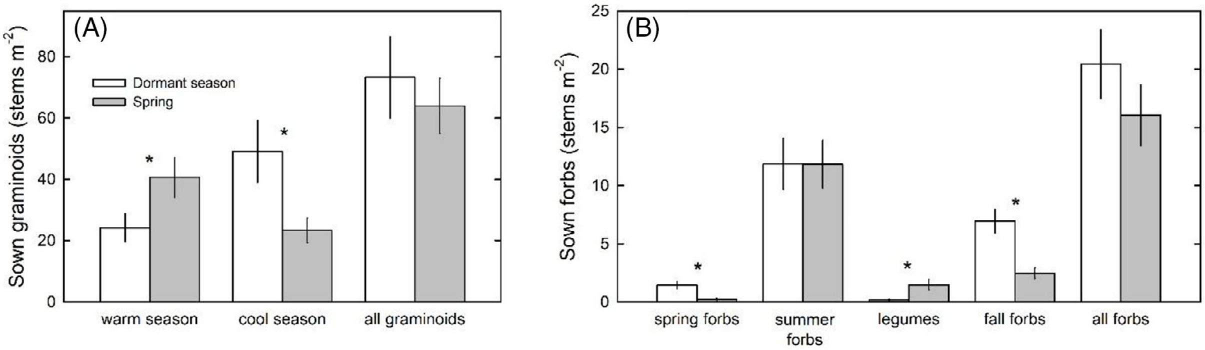

Figure 4. Differences in plant functional group composition in dormant-season and spring planted plots. Values presented are means (± SE) across all seed mixes and mowing treatments. Significant differences between spring and dormant-season plantings based on Tukey's post hoc tests are indicated with an *.

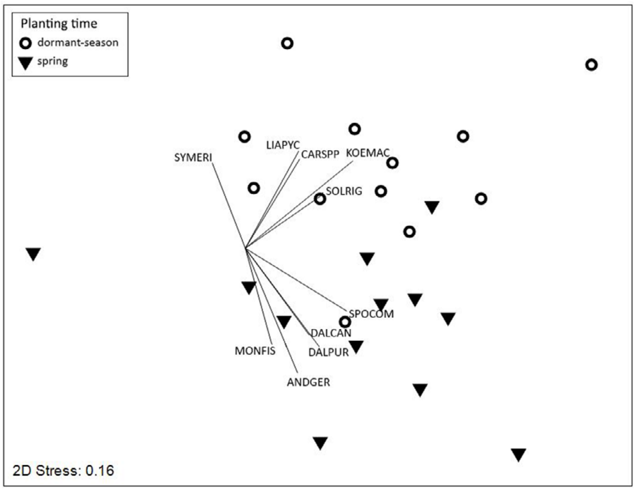

Figure 5. Non-metric multidimensional scaling (NMDS) of plant community composition in dormant-season and spring planted Pollinator mix plots. Vectors indicate species with Pearson correlations to NMDS greater than 0.40. Species include: ANDGER = *Andropogon gerardii*, CARSPP = *Carex* spp., DALCAN = *Dalea candida*, DALPUR = *Dalea purpurea*, KOEMAC = *Koeleria macrantha*, LIAPYC = *Liatris pycnostachya*, MONFIS = *Monarda fistulosa*, SOLRIG = *Solidago rigida*, SPOCOM = *Sporobolus compositus*, SYMERI = *Symphyotrichum ericoides*.

(Table S5; Fig. 3). Perennial weed and bare ground cover were higher with spring planting than with dormant-season planting (Fig. 3D) and sown plant cover was marginally higher ($p = 0.051$) with dormant-season planting than spring planting (Fig. 3A).

Planting Time Effects on Community Composition

Planting time did not influence the total number of graminoid or forb stems; however, it did influence functional group composition. Dormant-season planting favored the establishment of cool-season graminoids ($F_{1,29} = 6.18$, $p = 0.019$) and spring ($F_{1,29} = 12.0$, $p = 0.002$) and fall forbs ($F_{1,29} = 14.07$, $p = 0.001$), whereas spring planting favored the establishment of warm-season grasses ($F_{1,29} = 8.91$, $p = 0.006$) and legumes ($F_{1,29} = 10.0$, $p = 0.004$; Fig. 4).

Planting time had a strong effect on community composition in the Pollinator mix (PERMANOVA, Pseudo-$F_{1,23} = 3.73$, $p = 0.0004$; Fig. 5). Influential species favored by dormant-season planting included *Carex* spp., *Koeleria macrantha*, *Liatris pycnostachya*, *Solidago rigida*, *Symphyotrichum ericoides*, *Symphyotrichum novae-angliae*, *Symphyotrichum laeve*, and *Zizia aurea*; those favored by spring planting included *Andropogon gerardii*, *Dalea candida*, *Dalea purpurea*, *Monarda fistulosa*, *Ratibida pinnata*, *Rudbeckia hirta*, *Schizachyrium scoparium*, and *Sporobolus compositus* (see Table 1 for complete species list).

Cross-Site Comparison of Seed Mix Design and First-Year Mowing Effects

Differences in ecosystem service provision between seed mixes were comparable between this study and our previous study at a different site (Meissen et al. 2020). Erosion control, which was assessed using cover and stem density of sown species, was highest in the Economy mix and lowest in the Pollinator mix at both sites (Table 2). Weed resistance, which was assessed using the absence of weeds and absence of bare ground, was highest in the Economy and Diversity mixes and lowest in the Pollinator mix at both sites (Table 2). Weed cover was lowest in the Economy mix and highest in the Pollinator mix at both sites. Cover by bare ground was lowest in the Diversity mix and highest in the Pollinator mix at both sites. Pollinator resources, which were assessed using sown floral density and richness, were highest in the Diversity and Pollinator mixes and lowest in the Economy mix at both sites (Table 2). Inflorescence production was highest in the Pollinator mix and lowest in the Economy mix at both sites. Floral richness was highest in the Diversity mix at Nashua, highest in the Diversity and Pollinator mixes at Cedar Falls and lowest in the Economy mix at both sites.

Differences in ecosystem service provision between mowing treatments were also comparable between studies. In general, erosion control, weed resistance, and pollinator resources were higher in mown subplots than unmown subplots at both sites (Table 3). The average loss in ecosystem service provision in

Table 1. Plant species responsible for community dissimilarity between dormant-season and spring planted Pollinator mix plots. [a]Percentage of total dissimilarity contributed by each species. [b]Dormant-season and spring planted stem densities calculated from untransformed data.

Functional group	*Species*	*Contrib%[a]*	*Dormant-season[b] (stems/m²)*	*Spring (stems/m²)*
Spring forbs	*Zizia aurea*	3.69	1.42	0.58
	Penstemon digitalis	2.83	1.08	0.00
	Viola pedatifida	0.47	0.08	0.00
Summer forbs	*Rudbeckia hirta*	11.50	12.08	14.92
	Ratibida pinnata	4.79	1.75	2.00
	Monarda fistulosa	2.67	0.33	0.92
	Eryngium yuccifolium	1.57	0.33	0.33
	Drymocallis arguta	1.52	0.33	0.17
	Asclepias tuberosa	1.19	0.00	0.33
	Echinacea pallida	1.05	0.08	0.17
	Heliopsis helianthoides	0.48	0.00	0.08
	Silphium integrifolium	0.40	0.00	0.08
	Pycnanthemum virginianum	0.34	0.00	0.17
	Veronicastrum virginicum	0.33	0.08	0.00
	Silphium laciniatum	0.29	0.08	0.00
	Asclepias syriaca	0.24	0.00	0.08
Legumes	*Dalea purpurea*	2.56	0.00	1.25
	Dalea candida	2.04	0.00	0.75
Fall forbs	*Symphyotrichum ericoides*	5.42	2.67	0.25
	Symphyotrichum novae-angliae	5.29	2.92	2.67
	Symphyotrichum laeve	3.75	1.58	0.25
	Helenium autumnale	3.30	1.33	0.08
	Solidago rigida	2.52	1.08	0.00
	Vernonia fasciculata	2.00	0.25	0.58
	Liatris pycnostachya	1.54	0.33	0.00
	Symphyotrichum oolentangiense	0.99	0.17	0.08
	Solidago speciosa	0.56	0.08	0.00
Warm-season grasses	*Schizachyrium scoparium*	8.31	4.00	7.00
	Andropogon gerardii	7.97	0.75	5.50
	Sporobolus compositus	3.46	0.93	1.25
	Bouteloua curtipendula	1.79	0.00	0.92
Cool-season graminoids	*Carex* spp.	7.96	4.75	0.17
	Koeleria macrantha	7.15	7.92	1.58

Table 2. The impact of seed mix on ecosystem service provision at two study sites: Nashua and Cedar Falls (CF). For consistency between study sites, values are based on second year performance in spring planted plots only. At each site, the seed mix with the highest value for each variable was scored as a 100% and bolded for clarity and other seed mixes were scored as a relative proportion of the highest value.

		Economy mix		*Diversity mix*		*Pollinator mix*	
Service	*Attribute*	*Nashua*	*CF*	*Nashua*	*CF*	*Nashua*	*CF*
Erosion control	Sown cover	**100%**	**100%**	89%	88%	59%	62%
	Sown stem density	**100%**	**100%**	76%	78%	22%	38%
Weed resistance	Absence of weeds	**100%**	**100%**	82%	97%	61%	75%
	Absence of bare ground	90%	88%	**100%**	**100%**	69%	82%
Pollinator resources	Inflorescence production	9%	22%	46%	23%	**100%**	**100%**
	Sown floral richness	31%	79%	**100%**	**100%**	51%	**100%**

unmown subplots was also comparable between sites (Nashua = −38%, Cedar Falls = −28%; Table 3).

Discussion

In this study, we examined the impact of three management decisions (seed mix design, first-year mowing, and planting time) on ecological outcomes of conservation projects involving revegetation of native grass and forb species. Our results indicate that all three management decisions strongly influence vegetation outcomes during the early years of a revegetation project. Seed mix design and first-year mowing influence nearly every aspect of stem density and cover, while planting time influences floral richness and community composition. A cross-study comparison revealed remarkable consistency in the effects of seed mix design and first-year mowing, suggesting that the effect of

Table 3. The impact of first-year mowing on ecosystem service provision at two study sites: Nashua and Cedar Falls (CF). For consistency between study sites, values are based on second year performance in spring planted plots only. At each site, the mowing treatment with the highest value for each variable was scored as a 100% and bolded for clarity and the other mowing treatment was scored as a relative proportion of that percentage.

		Mow		*No mow*	
Service	*Attribute*	*Nashua*	*CF*	*Nashua*	*CF*
Erosion control	Sown cover	**100%**	**100%**	49%	68%
	Sown stem density	**100%**	**100%**	40%	52%
Weed resistance	Absence of weeds	**100%**	**100%**	40%	97%
	Absence of bare ground	82%	**100%**	**100%**	80%
Pollinator resources	Inflorescence production	**100%**	**100%**	41%	61%
	Sown floral richness	**100%**	**100%**	85%	77%

these management decisions are robust to moderate variation in site conditions, landscape context, and local climate, including annual rainfall.

Seed Mix Design. Grass-to-forb seeding ratio has a profound and predictable impact on ecological outcomes in conservation projects involving revegetation of native grass and forb species. Grass-dominated stands (e.g., the Economy mix) tend to have higher native cover, higher grass stem density, and lower weed abundance than forb-dominated stands (e.g., the Pollinator mix). Because of these attributes, moderately diverse, grass-dominated stands are well suited to conservation projects striving to minimize nutrient loss and erosion (Boyd 1942; Ellison 1950; Helmers et al. 2012), minimize weed invasion (Schramm 1990; Stevenson et al. 1995; Van der Putten et al. 2000), and provide cover for wildlife, such as USDA's Rare and Declining Habitat Conservation Practice (CP25) (USDA 2021). In contrast, forb-dominated stands tend to have higher forb stem density, higher floral richness, and higher floral abundance than grass-dominated stands. Because of these attributes, forb-dominated stands are well suited to conservation projects striving to provide high-quality pollinator habitat (Hopwood 2008; Pywell et al. 2011), such as USDA's Pollinator Habitat Conservation Practice (CP42) (USDA 2021). Our results are consistent with previous studies on the impact of grass-to-forb seeding ratio on native stem density and cover in restoration projects (e.g., Dickson & Busby 2009; Larson et al. 2011, 2017).

A site-customized, high-diversity, grass-to-forb balanced seed mix (e.g., the Diversity mix) has the potential to produce a vegetation community that is more multifunctional than either grass- or forb-dominated stands. Grass-dominated stands tend to provide erosion control and weed resistance but not pollinator resources; forb-dominated stands tend to provide pollinator resources but not weed resistance or erosion control. Our results suggest that a high-diversity, grass-to-forb balanced seed mix can effectively provide all three ecosystem services. Stem density and cover of sown species was comparable between the Diversity mix and Economy mix, suggesting that both would provide effective erosion control and weed resistance. The Diversity mix also had comparable forb stem density and floral richness to the Pollinator mix, suggesting that both would provide high-quality pollinator habitat. While pollinator communities were not measured directly in the current study, research suggests that communities with higher floral richness tend to attract a more diverse assemblage of pollinators (Hopwood 2008; Pywell et al. 2011; Myers et al. 2012). Although the Pollinator mix had higher sown floral density than the Diversity mix, this result was largely driven by two, highly abundant species: *R. hirta* (>75% of inflorescences in the Pollinator mix) and *R. pinnata* (8.5% of inflorescences in the Pollinator mix; data not shown). *R. hirta* is an early successional species that tends to become less common in stands with time (Williams et al. 2007), suggesting that floral density would likely decrease with time in the Pollinator mix as well. Because of its capacity to simultaneously provide erosion control, weed resistance, and pollinator resources, we recommend a site-customized, high-diversity, grass-to-forb balanced seed mix to any land manager striving for whole ecosystem restoration of native tallgrass prairie.

First-Year Mowing. First-year mowing facilitates native plant establishment during the early stages of a revegetation project. Across seed mixes, first-year mowing increased graminoid stem density, forb stem density, cover by sown plants, sown species richness, and weed resistance. The consistency of these effects across seed mixes suggests that first-year mowing can enhance the provisioning of ecosystem services in many different settings. High establishment rates during the early years of a restoration project can have a long lasting influence on the restored community. Previous studies have shown that non-native species can outcompete native prairie species if they establish first (Dickson et al. 2012; Wilsey et al. 2015), suggesting that priority effects shape reconstructed prairie communities (Temperton & Hobbs 2004). Nevertheless, many land managers do not mow during the early years of a tallgrass prairie restoration (Rowe 2010). In addition to native plant establishment, first year mowing also increased floral density and richness. Because CRP contracts typically last only 10–15 years, improvements in the provisioning of floral resources in the early years of a conservation project would help maximize its lifetime value as pollinator habitat on the landscape. Future research should examine whether the beneficial effects of first year mowing also occur at restoration sites with slower growing vegetation (e.g., mixed-grass prairie, short-grass prairie).

Planting Time. Dormant-season planting could be a beneficial management practice for pollinator enhancement projects for several reasons. First, stands planted in the dormant-season had higher floral richness than stands planted in the spring. Floral richness is a key determinant of pollinator habitat quality (Hopwood 2008; Pywell et al. 2011; Myers et al. 2012). Second, stands planted in the dormant-season had more cool-season graminoids and fewer warm-season grasses than stands planted in the spring. Grasses are typically seeded at low rates in pollinator habitat conservation projects to reduce competition for native forbs (USDA 2021). Some C_4 perennial grasses, such as big bluestem (*A. gerardii*) are known to outcompete forbs (Grman et al. 2021), suggesting that planting in the dormant-season would improve forb persistence. Third, stands planted in the dormant-season had more spring forbs and fall forbs than stands planted in the spring. Past research on pollinator habitat restoration has shown that the timing of nectar production can be just as important as total nectar production in restored plant communities (Timberlake et al. 2019) and that restoration sites in agricultural landscapes often produce plant communities with low nectar availability early and late in the growing season (Havens & Vitt 2016; Timberlake et al. 2019). One goal of the Pollinator Habitat Conservation Practice (CP42) is to establish a minimum of three flowering species during each of three different seasonal bloom periods (spring, summer, fall) throughout the growing season (USDA 2021). By improving establishment of spring and fall forbs, dormant-season planting would increase the probability of achieving this goal. Fourth, stands planted in the dormant-season had fewer perennial weeds and less bare ground than stands planted in the spring. Perennial weeds are a major concern in conservation projects because they reduce native richness and diversity (Blumenthal et al. 2003; Martin & Wilsey 2012) and increase long-term management costs. We recommend dormant-season planting to land managers striving to enhance pollinator habitat. Our results are consistent with previous studies in showing that planting time has minimal effects on overall stem density but influences native species establishment (Peters & Schottler 2010; Boeck Crew et al. 2020) and community composition (Larson et al. 2011, 2017).

One caveat about our recommendation for dormant-season planting relates to the establishment of milkweeds (*Asclepias* spp.). Milkweed establishment is an important goal of many pollinator habitat conservation projects because they are larval host plants for the eastern migratory monarch (*Danaus plexippus plexippus*) butterfly (Thogmartin et al. 2017). Previous research has shown that some milkweed species are more abundant in conservation grasslands where they were seeded than in sites where they were not sown (Lukens et al. 2020), and increasing milkweed stem density in the agricultural landscape by including them in restoration plantings is a goal in monarch conservation initiatives (Monarch Joint Venture 2021). In contrast to our general conclusion that dormant-season planting would be a beneficial strategy for enhancing pollinator habitat, stands planted in the dormant-season had lower milkweed establishment. At least one milkweed species (*Asceplias syriaca* or *A. tuberosa*) was present in 67% of spring planted plots compared to 33% of dormant-season plots (Fisher's exact test, $p = 0.22$), and milkweed stem density was significantly greater in spring planted plots (0.42 stems/m^2) than in dormant-season plots (0.00 stems/m^2; Kruskal–Wallis, $H_1 = 4.57$, $p = 0.033$). Spring planting may have favored milkweed establishment for a variety of reasons. Seeds planted in the dormant-season are more vulnerable to predation (Howe & Brown 1999; Pellish et al. 2018; Riebkes et al. 2018), parasitism by microorganisms (fungal and bacterial decomposition), seed senescence (Chambers & MacMahon 1994; Blaney & Kotanen 2002; Clark & Wilson 2003), and environmental causes of seed loss (e.g., wind, rain) than seeds planted in the spring. It is also possible that higher establishment rates of other species in dormant-season plantings resulted in increased competition for germinating milkweed plants. While we still advocate for dormant-season planting in pollinator habitat conservation projects, we also recommend that landowners increase milkweed seeding rates to overcome their lower establishment rates.

Cross-Study Comparison of Management Effects. Many studies implement experiments at a single location which can result in outcomes reflecting local site conditions instead of treatment differences (Gibson et al. 1993). Our cross-study comparison revealed remarkably consistent effects of seed mix design and first-year mowing, suggesting that these management effects have a greater impact on project outcomes than local site conditions. The Economy, Diversity, and Pollinator mixes displayed the same relative ranking at Cedar Falls and Nashua for all six traits used to assess ecosystem service provision. Furthermore, the standardized scores for each trait × seed mix combination were similar between sites (average difference in standardized score between Cedar Falls and Nashua = 11%). In the Nashua study (Meissen et al. 2020), we recommended the Diversity mix to land managers striving for whole ecosystem restoration because of its capacity to effectively provide erosion control, weed resistance, and pollinator resources. Our cross-study comparison only increases our confidence in this recommendation. Forb-dominated seed mixes, such as the Pollinator mix, provide high-quality pollinator habitat but their low native cover and high susceptibility to weed invasion are unattractive attributes for restoration projects in general. First-year mowing improved ecosystem service provisioning at both sites to a comparable degree. We recommend this approach in Midwestern revegetation projects involving native grasses and forbs because of its capacity to simultaneously enhance the provisioning of all three ecosystem services (erosion control, weed resistance, and pollinator resources).

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Supporting Information

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

Table S1. Species list and seeding rates of the Economy mix (3:1 grass-to-forb seeding ratio) at the Northeast Research and Demonstration Farm (Nashua) and University of Northern Iowa's Tallgrass Prairie Center (Cedar Falls).
Table S2. Species list and seeding rates of the Diversity mix (1:1 grass-to-forb seeding ratio) at the Northeast Research and Demonstration Farm (Nashua) and University of Northern Iowa's Tallgrass Prairie Center (Cedar Falls).
Table S3. Species list and seeding rates of the Pollinator mix (1:3 grass-to-forb seeding ratio) at the Northeast Research and Demonstration Farm (Nashua) and University of Northern Iowa's Tallgrass Prairie Center (Cedar Falls).
Table S4. Effects of seed mix, mowing, and planting time on five plant community characteristics.
Table S5. Effects of seed mix, mowing, and planting time on percent cover of sown plants, unsown native plants, annual weeds, perennial weeds, and bare ground.
Table S6. Unsown species, classified vegetation type and origin included in cover estimates.

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