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RESEARCH ARTICLE

Forb Species Establishment Increases with Decreased Grass Seeding Density and with Increased Forb Seeding Density in a Northeast Kansas, U.S.A., Experimental Prairie Restoration

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Abstract

Most prairie restorations fail to produce the diversity of species found in unplowed remnants. This lack of restored diversity is hypothesized to be partly due to the inhibition of forb species by high seeding densities of dominant grasses and partly due to the low seeding densities of forbs used in many restorations. We tested this hypothesis by sowing various densities of forb and warm-season grass seeds into a restoration begun on bare soil. This is the first replicated restoration experiment we are aware of that varies grass seeding densities to examine the effects on forbs. Four years after seeding, we found that higher densities of grass seeds decreased forb cover, biomass, and richness, and higher densities of forb seeds increased forb richness. These results suggest that dominant grasses compete strongly with native forb species and that many forb species thrive when they are spatially separated from dominant grasses. The results also suggest that seed availability limits the establishment of some forbs. Forb diversity can therefore be increased by decreasing grass seeding density, by increasing forb seeding density, or both. However, forb seeds are generally expensive, and increasing forb seeding density across the entire area of a restoration may be prohibitively expensive. We therefore recommend a low seeding density of dominant grasses, and we recommend spatially separating forbs from dominant grasses by adding most forb seeds to areas with little to no dominant grasses and by adding the rest of the forb seeds to areas with a low density of dominant grasses.

Key words: **conservative forb species richness, Conservation Reserve Program, grassland, optimal seed mix, weedy species.**

Introduction

Prairie restorations generally fail to produce the diversity of plant species found in prairie remnants (Weber 1999; Polley et al. 2005; but see Pfeiffer 1999; Whitney 1999). Restorations in other parts of the world also generally fail to produce plant diversity similar to remnant levels (Lockwood & Pimm 1999; Walker et al. 2004). This lack of restored diversity is largely due to a lack of establishment from forbs (broadleaf herbs). Forbs are the most diverse group of plant species in the tallgrass/mixed-grass prairie. They comprise at least 60% of the plant species in remnant areas of Konza Prairie in northeastern Kansas (Collins et al. 1998) and the proportion increases to the east of Konza. Comparatively low forb establishment in restorations may be due to low seeding richness and density of forbs (Seabloom et al. 2003; Sheley & Half 2006) or to the inhibitory effects of seeding high densities of dominant grasses (Weber 1999; Kindscher & Fraser 2000).

"Conservative" species are also generally absent from restorations. Conservative species are rarely found outside undisturbed remnant plant communities and can be thought of as late successional (Swink & Wilhelm 1994). These species are hypothesized to be inhibited by high densities of dominant grasses and other aggressive species (Packard 1997).

Although it is recognized that high densities of dominant grasses may hinder the establishment of forbs (Kindscher & Fraser 2000) and conservative species (Weber 1999), there are several reasons many prairie restorationists continue to seed dominant grasses at high densities. Restorationists have been influenced by the agricultural practice of planting high densities of dominant grasses as a way to reduce soil erosion (Boyd 1942; Jelinski & Kulakow 1996). Planting high densities of dominant grasses is championed in restoration by the "prairie matrix" concept (Betz 1986; Betz et al. 1999) and other planting strategies (Wilson 1970; Schramm 1992) as a method to control weedy species and improve soil characteristics. A high density of grass seed also costs very

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little because grass seed is generally much less expensive than forb seed.

Few explicit tests of the effects of dominant prairie grasses on forb species have been completed, but Kindscher and Fraser (2000) report that areas sown without grass seeds contain 84.6% forb cover (both sown and nonsown species) and higher species richness than areas sown with grass seeds (18.2% forb cover). Also, plant species diversity appears to stay the same or slightly decline over time in sites initially sown with high densities of grass and dominant prairie species (Sluis 1999). In other studies, forbs do not establish well when seeded into intact stands of grass (Williams et al. 2007), even though transplants have moderate establishment success (Warkins & Howell 1983; Brown & Bugg 2001). Previous studies do not examine whether low densities of grass allow greater forb establishment than high densities of grass. Also, in the study most similar to the experiment presented here (Kindscher & Fraser 2000), the no grass treatment is not truly replicated because it is on a strip of land that accidentally does not receive grass seeds.

Low seeding densities of forb seeds may also decrease forb abundance and richness (Seabloom et al. 2003; Sheley & Half 2006). Many of the most difficult forb species to establish from seed also have very expensive seed. As a result, these species are often seeded at low density or not at all. Increasing the seeding density of these forb species may therefore increase their abundance and richness.

Although we focus on forb species establishment, we also examine whether seeding density affects weed abundance (Betz 1986; Schramm 1992) and whether seeding density affects bare ground. Competition from certain weeds can dramatically reduce prairie establishment (Blumenthal et al. 2003), and increased bare ground can increase soil erosion (Ellison 1950) and the spread of weeds (Bergelson et al. 1993) while also aiding the establishment of some seeded species (Gross 1984).

We manipulate both grass and forb seeding density, but not seeding richness, in our experiment. The objective for the study is to find the level of grass and forb seeding density that will maximize forb abundance and richness. Our hypothesis is that higher grass seeding density will decrease forb establishment, and higher forb seeding density will increase forb establishment only at low grass sowing density (forb × grass sowing density interaction). We also examine whether abundant forb species are decreasing the percentage cover of other forb species.

Methods

Study Site

This experiment was located in northeast Kansas approximately 28 km southeast of Lawrence (lat 95°08′W, long 38°49′N), within a 6.1-ha field that was used for agriculture from the 1960s until 2000. The field surrounding the experiment was enrolled in the Conservation Reserve Program (CRP; Jelinski & Kulakow 1996) and seeded to native species in 2001, several days before the experimental area received any seeds. Management during the study period consisted of mowing the entire field (including the experiment) to approximately 17.8 cm height in July 2001 and June 2002 and conducting a controlled burn in March 2003. Soil at the site was Sibleyville Loam with 3–7° slopes (Dickey et al. 1977). The soil was derived from sandstone and loamy shale and has experienced some erosion. The climate of the region was humid continental, with mean annual temperature of 12.7°C and mean annual precipitation of 952 mm. Seasonal temperatures can be extreme, with minimum temperatures in winter as low as −29°C and maximum temperatures in summer as high as 43°C. The seasonal distribution of precipitation was unimodal, peaking in June (Kettle & Whittemore 1991). According to the U.S. drought monitor, there were no drought conditions during the growing seasons of 2001 and 2004, but there were abnormally dry to severe drought conditions from July to October 2002 and abnormally dry to extreme drought conditions from July to October 2003 (NDMC, USDA, and NOAA 2008).

Field Methods

All seeds in the experiment were sown at densities relative to the densities of purchased seeds in the surrounding CRP planting (ambient density). Grass seeds (0.5× ambient density; 2× ambient density) and forb seeds (2× ambient density; 8× ambient density) were sown on bare soil in a factorial design. We also added one treatment with no grass and 8× ambient forb seed density. We hereafter refer to 0.5× grass density and 2× forb density as low density, and we refer to 2× grass density and 8× forb density as high density. Low density of grass seed was 0.08 g/m^2 of *Tripsacum dactyloides* and 0.42 g/m^2 of all other grasses combined (Table 1; 1 $g/m^2 = 8.92$ pounds per acre). Low density of forb seed was 0.18 g/m^2 of *Dalea purpurea* and 0.42 g/m^2 of all other forbs combined. The low and high densities bracket Diboll's (1997) recommended seeding rates for tall-prairie plantings. Low densities were approximately half the recommended weight of grasses and of forbs, whereas high densities were approximately twice the recommended weight. The number of seeds added at low density was lower for grasses than for forbs, with approximately 1 *T. dactyloides* seed/m^2 and 150 seeds/m^2 of all other grasses combined, and 96 *D. purpurea* seeds/m^2 and 184 seeds/m^2 of all other forbs combined. The number of seeds was estimated from the seed weights listed in the 2007 Prairie Moon Nursery catalog (Winona, MN, U.S.A.).

Seeds were hand-broadcast into the experiment and raked into the soil on 21 May 2001. All seeds were purchased from Missouri seed companies (Hamilton's in Elk Creek, Wildflower Nursery in Jefferson City, and Sharp Brothers in Clinton). All seeds from Hamilton's and Wildflower Nursery were collected in Missouri, whereas some

Table 1. The low density seeding weight of seeds purchased from Missouri seed companies and the constant density of seeds hand collected from a native prairie near to the restoration (1 g/m^2 = 8.92 pounds/acre).

Scientific Name	*Common Name*	*Purchased (g/m^2)*	*Collected (g/m^2)*	*Abundance (%)*
Andropogon gerardii	Big bluestem	0.126	0	28 (26.3)
Baptisia alba	White wild indigo	0.005	0	2 (0.5)
Bouteloua curtipendula	Sideoats grama	0.101	0	21 (3.4)
Brickellia eupatorioides	False boneset	0	Trace	6 (0.9)
Chamaecrista fasciculata	Showy partridge pea	0.070	0	30 (9.0)
Coreopsis tinctoria	Plains coreopsis	0.003	0	
Desmanthus illinoensis	Illinois bundleflower	0.131	0.004	27 (1.3)
Desmodium species		0	Trace	2 (3.7)
Dracopis amplexicaulis	Clasping coneflower	Trace	0	
Echinacea purpurea	Purple coneflower	Trace	0	
Gaillardia pulchella	Indian blanket	0.004	0	
Helianthus grosseserratus	Sawtooth sunflower	0	Trace	1 (2.0)
H. maximiliani	Maximilian sunflower	0.033	0	30 (15.7)
Liatris punctata	Dotted gayfeather	Trace	0	
Oenothera species		0	Trace	8 (1.0)
Oligoneuron rigidum	Stiff goldenrod	0.006	0.003	
Panicum virgatum	Switchgrass	0.013	0	27 (11.1)
Pascopyrum smithii	Western wheatgrass	0.042	0	14 (0.9)
Penstemon digitalis	Foxglove beardtongue	0.011	0	1 (0.4)
Pycnanthemum tenuifolium	Slender-leaved mountain mint	0	0.002	
Ratibida columnifera	Prairie coneflower	0.011	0	29 (1.2)
R. pinnata	Grayhead prairie coneflower	0.016	0	16 (6.0)
Rudbeckia hirta	Black-eyed Susan	0.001	0	11 (0.4)
Salvia azurea	Pitcher sage	0.021	0	
Schizachyrium scoparium	Little bluestem	0.067	0	18 (3.8)
Silphium integrifolium	Rosinweed	0.005	0.005	
Si. laciniatum	Compass plant	0	Trace	
Sorghastrum nutans	Indiangrass	0.076	0	29 (20.4)
Symphyotrichum novae-angliae	New England aster	0.001	0	
Tradescantia ohiensis	Ohio spiderwort	0.001	0	3 (0.4)
Tripsacum dactyloides	Eastern gammagrass	0.075	0	
Vernonia baldwinii	Western ironweed	0	Trace	2 (0.5)
Zizia aurea	Golden Alexanders	0.005	0	
Conservative species				
Amorpha canescens	Lead plant	Trace	0.008	9 (0.7)
Asclepias tuberosa	Butterfly milkweed	0.005	0	10 (1.9)
Coreopsis lanceolata	Lanceleaf coreopsis	0.003	0	
Dalea candida	White prairie clover	0.021	0.004	8 (0.5)
D. purpurea	Purple prairie clover	0.182	0.002	25 (0.8)
Echinacea angustifolia	Black Sampson	Trace	0	
Ec. pllida	Pale purple coneflower	Trace	0.008	
Eryngium yuccifolium	Rattlesnake master	0	0.008	
Helianthus mollis	Ashy sunflower	0.011	0.002	8 (1.9)
Lespedeza capitata	Round-headed bush clover	0.022	0.003	18 (1.3)
Li. aspera	Tall gayfeather	Trace	0.003	
Li. pycnostachya	Prairie blazing star	0.011	0	
Mimosa nuttallii	Catclaw sensitive briar	0.011	Trace	2 (0.6)
Sporobolus heterolepis	Prairie dropseed	0	Trace	
Symphyotrichum oolentangiense	Sky-blue aster	0.002	0	
Tephrosia virginiana	Goat's rue	0.005	0	

The abundance column represents the number of quadrats in 2004 that contained a given species in either the spring or summer sampling period (empty cells denote the absence of the species). The number in parentheses in the abundance column represents the average 2004 percentage cover in only the quadrats where the species was found. The species are listed in a group with coefficients of conservatism greater than five (conservative species) and a group containing all other species. Rows that are shaded represent pure live seed weight, and other rows and hand-collected seed represent bulk weight.

seeds from Sharp Brothers may have been collected outside Missouri. Several species hand collected from a prairie 1 km from the experiment were also hand-broadcast into the entire 6.1-ha CRP site (including the experiment) in late May 2001 (Table 1). These hand-collected seeds were sown to increase the species richness of sown seeds and to incorporate locally collected seeds. Hand-collected seeds were sown at uniform densities across all treatments and should not change the effects of experimental treatments. Only purchased seeds were sown at densities higher or lower than ambient density. All five treatments were replicated six times in a randomized complete block design (Manly 1992). Each replicate consisted of a 2 × 2–m plot. Plots were laid out side by side in a 10 × 12–m area. Vegetation data were collected from a 1 × 1–m quadrat within the center of each plot.

We sampled vegetation in the late spring (May or June) and the late summer (August or September) from the end of the first growing season (2001) to the end of the fourth growing season (2004). We estimated the percentage of ground within the quadrat that each species covered (nomenclature follows Kartesz 1999). We also estimated the percentage cover of bare ground and dead litter that was visible while standing above the vegetation canopy. The percentage cover of all species, bare ground, and litter within a quadrat could sum to more than 100% if the canopy layers of the vegetation overlapped.

To calculate values in Table 1 for the number of quadrats each species occupied, we combined spring and summer 2004 data and then removed duplicate occurrences within each quadrat. For all statistical analyses, annual estimates of species richness and percentage cover were derived by averaging data from spring and summer samples each year. We averaged species richness across the spring and summer, rather than summing the number of different species found, to calculate the species richness likely to be present at one given sampling date. The statistical significance of treatment effects was the same whether richness data were averaged or summed. Data from 2001 were not presented because data from this year were not collected in the spring and results were generally the same as in 2002.

Aboveground biomass was collected from 13 to 17 August 2004. Two 100 × 7.6–cm strips of biomass were clipped to ground level within each quadrat, and the biomass was sorted within 3 days of clipping to grass, forbs, and dead vegetation litter. Sorted biomass was placed into paper bags and dried at 74°C for 96 hours before being weighed.

Data Analysis

All analyses were completed using SPSS version 13.0 for Windows, and using type III sum of squares ($\alpha = 0.05$). To improve normality and homoscedasticity, the data for percentage cover of sown grasses were square root transformed, and all biomass data were $\log_{10}$ transformed. All other data were untransformed. Within each year, we analyzed the data using a two-way analysis of variance (ANOVA) with two levels of grass sowing density (low and high) and two levels of forb sowing density (low and high). A blocking term was included with all ANOVA analyses, but this term was removed if it was not significant. The treatment containing no grass seed (no grass; high forb density) was compared to the other four treatments using the least significant difference (LSD) method with $\alpha =$ 0.0125 to create an experimentwise $\alpha = 0.05$ (the error term in this analysis was from a one-way ANOVA of all five treatments; Sokal & Rohlf 1995). We used Pearson correlation to examine the relationship between 2004 untransformed litter and grass biomass across all five treatments.

The average 95% confidence intervals (CIs) presented in the figures were calculated using an average standard error equal to: (square root [mean square error term from within-year one-way ANOVA/number of replicates per treatment]). When calculating 95% CIs for transformed data, we back transformed the CIs.

To examine whether individual forb species were competitively decreasing the percentage cover of other forbs, we performed analysis of covariance with all five treatments (30 plots) in the spring and summer of 2002–2004. During each time period, we used percentage cover of sown forbs (minus the forb included as the covariate) as the response variable, the five treatments as a fixed factor, and all sown forb species with greater than 10% average cover as the covariate. We included the five treatments as a fixed factor to account for the effects of treatments that would not be due to the forb covariate (i.e., we needed to account for higher forb sowing density increasing forb percentage cover and higher grass sowing density decreasing forb percentage cover). We also used the same method to examine the effects of several grass species on sown forb percentage cover in the summer of 2002–2004, except we used the percentage cover of a grass species as the covariate in these analyses.

We examined the effects of treatments on conservative forb richness by considering only those forb species with conservatism values above five. Conservatism values ranged from a high of 10 for species only found in undisturbed remnant vegetation to a low of 0 for generalist species. The conservatism values were assigned by the consensus of 17 Kansas botanists, as described by Freeman and Morse (2002) and Jog et al. (2006).

Results

In all statistical tests, grass and forb sowing density never interacted significantly to affect any response variable.

Abundance

Sown Grass Abundance. From 2002 to 2004, the average percentage cover of sown grasses stayed at 2% in the no grass sowing treatment but increased from 26 to 70% in treatments where grass was sown, as shown in Figure 1A. Within years, sowing grass at high density led to a significant increase in 2002–2004 sown grass cover. Increasing forb sowing density led to a small but significant decrease in sown grass cover in 2003 but had no significant effect in

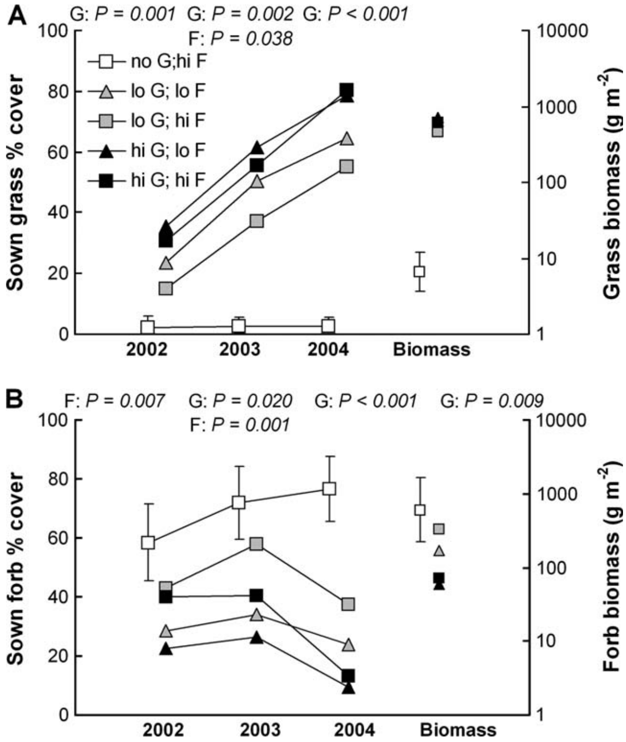

Figure 1. Abundance of sown grasses (A) and sown forbs (B) as represented by percentage cover in 2002–2004 on the left side of each graph and 2004 biomass on the right side of each graph (note the scale for biomass is logarithmic; error bars around the no grass treatments represent the average 95% CI for all treatments within a particular year; *p* values represent the significance of grass and/or forb sowing density for two-way within-year ANOVAs that do not include the no grass treatment; lo, low seeding density; hi, high seeding density; G, grass; and F, forb).

2002 or 2004. Grass biomass, as measured in 2004, did not differ significantly between treatments when grass seeds were sown (Fig. 1A). Not surprisingly, when grass seeds were not sown, the cover and biomass of sown grasses was significantly lower in all years compared to all other treatments (LSD method).

Sown Forb Abundance. From 2002 to 2004, the average percentage cover of sown forbs increased from 58 to 77% in the no grass sowing treatment but increased from 33 to 40% in 2002–2003 and then decreased from 40 to 21% in 2003–2004 in treatments where grass was sown, as shown in Figure 1B. Within years, increasing forb sowing density led to a significant increase in 2002 and 2003 sown forb cover but had no significant effect in 2004. Sowing grass at high density led to a significant decrease in 2003 and 2004 sown forb cover, did not significantly affect sown forb cover in 2002, and led to a significant decrease in 2004 forb biomass (Fig. 1B). When grass seeds were not sown, the cover of sown forbs was significantly higher than all other treatments in 2004, significantly higher than all treatments except the low grass/high forb treatment in 2003, and significantly higher than all low forb treatments in 2002 (LSD). When grass seeds were not sown, forb biomass in 2004 was significantly higher than all other treatments except the low grass/high forb treatment (LSD).

Total Biomass. Total live aboveground biomass was equal to the sum of grass biomass and forb biomass. No treatments significantly affected 2004 total live aboveground biomass or 2004 total aboveground biomass including litter. The average 2004 total live aboveground biomass in all plots was 725 g/m^2.

Percentage Cover of Individual Species. We examined the effects of sown forb species with greater than 10% average cover (*Ratibida columnifera* in the spring of 2002–2003 and summer of 2002, *Chamaecrista fasciculata* in the summer of 2002–2004, and *Helianthus maximiliani* in the summer of 2002–2004 and spring of 2003–2004) on the percentage cover of the remaining sown forb species (data not shown). In the spring of 2003, there was a significant negative relationship between the percentage cover of *H. maximiliani* and the remaining sown forb species ($p = 0.001$) and between the cover of *R. columnifera* and the remaining forb species ($p < 0.001$), when also taking into account treatment effects ($p < 0.001$ for both species). In the summer of 2004, the relationship between the cover of *C. fasciculata* and the remaining sown forb species was significantly different in different treatments (*C. fasciculata* covariate × treatment $p = 0.039$; treatment $p < 0.001$; *C. fasciculata* covariate $p = 0.641$). There was a significant negative regression between the cover of *C. fasciculata* and the remaining forb species in the no grass sowing treatment (slope $= -0.727$; $p = 0.014$) but no significant regressions in the other treatments. No other relationships were significant.

There was just one significant relationship in the summers of 2002–2004 between the percentage cover of any of the five most abundant sown grasses (*Andropogon gerardii*, *Schizachyrium scoparium*, *Bouteloua curtipendula*, *Panicum virgatum*, and *Sorghastrum nutans*) and the percentage cover of sown forbs. In the summer of 2003, there was a significant negative relationship between the cover of *S. nutans* and the cover of sown forbs ($p = 0.015$) when also taking into account treatment effects ($p = 0.004$).

Percentage Cover of Nonsown (Weedy) Species. From 2002 to 2004, the average percentage cover of nonsown species decreased from 14 to 2% across all treatments, as shown in Figure 2. Within years, high forb sowing density and high grass sowing density both led to a decrease in 2003 nonsown cover when also accounting for the blocking effect ($F_{[5,15]} = 4.19$; $p = 0.014$). No treatment significantly affected the cover of nonsown species in 2002 or 2004. When grass seeds were not sown, the cover of nonsown species was never significantly different from treatments where grass seeds were sown (LSD).

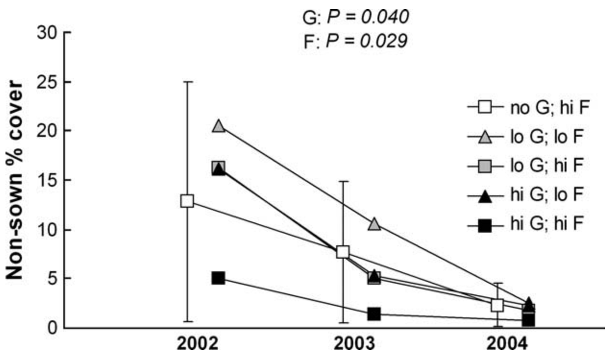

Figure 2. Percentage cover of nonsown species (error bars around the no grass treatments represent the average 95% CI for all treatments within a particular year; p values represent the significance of grass and forb sowing density for a two-way within-year ANOVA that does not include the no grass treatment; lo, low seeding density; hi, high seeding density; G, grass; and F, forb).

Percentage Cover of Bare Ground. From 2002 to 2004, the percentage cover of bare ground increased from 4 to 24% in the no grass sowing treatment but showed an increase in 2002–2003 from 4 to 16% followed by a decrease in 2003–2004 from 16 to 9% at low grass density and showed an increase in 2002–2003 from 2 to 11% followed by a decrease in 2003–2004 from 11 to 4% at high grass density (data not shown). The amount of bare ground may have been affected by litter because litter biomass increased when grass biomass increased ($r = 0.534$; $p = 0.002$; data not shown).

Richness

Sown Forb Richness. From 2002 to 2004, the average richness of sown forb species increased from 6.8 to 9.4 species in the no grass sowing treatment but increased from 5.8 to 6.2 species in 2002–2003 and then decreased from 6.2 to 5.5 species in 2003–2004 in treatments with high grass sowing density, as shown in Figure 3A. Within years, high forb sowing density significantly increased sown forb richness in 2002–2004, and high grass sowing density did not significantly affect forb richness in 2002 and 2003 but led to a significant decrease in 2004 forb richness. When grass seeds were not sown, the richness of sown forbs was significantly higher than all other treatments except the low grass/high forb treatment in 2004 and significantly higher than all low forb treatments in 2002 and 2003 (LSD).

Conservative Sown Forb Richness. From 2002 to 2004, the average richness of sown forb species with coefficients of conservatism greater than five hardly changed in treatments with low forb sowing density but increased from 1.6 to 2.4 species in treatments with high forb sowing density, as shown in Figure 3B. In 2004, when grass seeds were not sown, the richness of conservative sown forb species was significantly higher than all treatments with low forb density (LSD). No other treatments significantly affected conservative sown forb richness in any year.

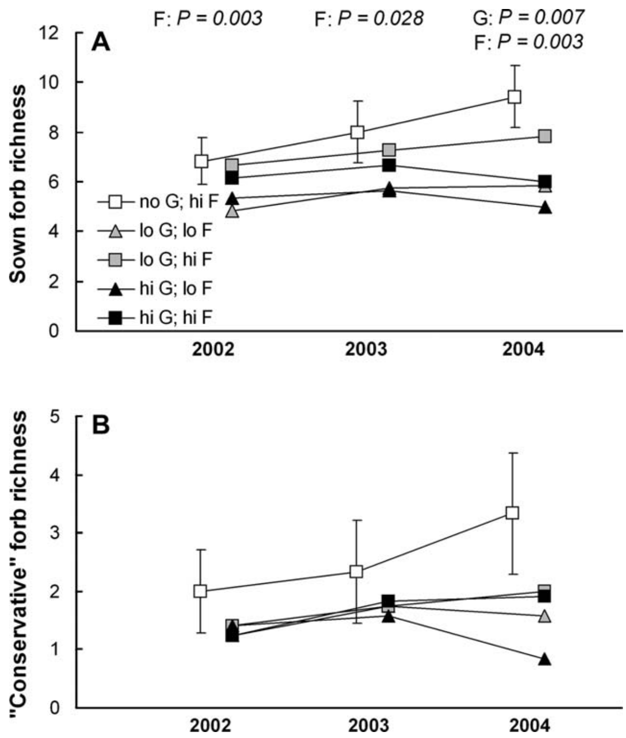

Figure 3. Species richness as represented by (A) sown forb richness and (B) sown richness of "conservative" forb species (defined as forb species with a coefficient of conservatism greater than five; error bars around the no grass treatments represent the average 95% CI for all treatments within a particular year; p values represent the significance of grass and/or forb sowing density for two-way within-year ANOVAs that do not include the no grass treatment; lo, low seeding density; hi, high seeding density; G, grass; and F, forb).

Discussion

Grass species dominate the seed mix (by weight and total number of seeds) in many prairie restorations. Our results suggest that this will lead to a rapid increase in dominant grass abundance that will cause a moderate decrease in forb species richness and a dramatic decrease in forb species abundance. Seed mixes with low forb seed density also appear to limit the presence of some forb species. Grass and forb seeding densities appear to affect conservative forb species richness in a qualitatively similar manner to overall sown forb richness.

Forb richness will likely increase due to both decreasing grass seeding density and increasing forb seeding density. We recommend seeding the highest possible density of subdominant forbs. However, the high cost of forb seeds may prevent many restorationists from substantially increasing forb seeding density. Also, increasing forb seeding density in the presence of high grass seeding density may ultimately have no effect on forb abundance, given that forb cover and biomass were strongly limited by high grass seeding density in the final year of our study. Forb species established best in the treatment without grass seeds, suggesting that spatial separation of expensive forb seeds from dominant grasses may be most economical. In areas that do receive dominant grass seed, it is advisable to keep grass seed densities low to increase forb abundance and richness.

The spatial separation of grasses and forbs may favor forb establishment. Spatial separation may be maintained in nature via a competition/colonization trade-off. Some species cannot coexist in direct competition with dominant species, but they are able to avoid direct competition by dispersing seeds farther than dominant species and colonizing separate sites (Hutchinson 1951; Tilman 1994; Turnbull et al. 1999). If it is true that many species exist by colonizing sites away from dominant species, then the restoration practice of sowing all species everywhere and sowing dominant species at high densities may be counterproductive to achieving high species diversity. The method of sowing forbs away from dominant grasses in some places (Schramm 1992) may help to mimic the natural patchiness of species usually caused by a competition/colonization trade-off, and this planting method may increase the diversity of the final restoration by allowing less-competitive species to establish away from dominant grasses. Animal grazing may also cause spatial heterogeneity that may increase forb establishment (Collins & Barber 1986; Vinton et al. 1993; Martin & Wilsey 2006), but many restorations do not have large amounts of animal disturbance and should therefore incorporate heterogeneity into the planting design.

We focus on the overall effects of grass sowing density because our study was designed to test the effects of sown grasses on sown forbs and vice versa. Consequently, any tests of the effects of individual forb species on other forbs are likely to have low statistical power. However, there is evidence that certain forb species (*Helianthus maximiliani*, *Ratibida columnifera*, and *Chamaecrista fasciculata*) decrease the abundance of other forb species. As such, it may be wise to limit the sowing density of dominant forbs as well as dominant grasses when the establishment of subdominant species is a high priority.

Although seeding densities had large effects on sown forbs and grasses, weedy (nonsown) species abundance dramatically declined at all seeding densities. It is surprising that treatments without grass seeds also had low cover of weedy species, given that high dominant grass seeding density is a proposed method for weed control (Wilson 1970; Betz 1986; Schramm 1992). However, it is likely that several forb species (*H. maximiliani*, *R. columnifera*, and *C. fasciculata*) were strong enough competitors to replace weedy vegetation. The most common weedy species in 2002 were the foxtail grasses, Chinese foxtail (*Setaria faberi*) and Yellow foxtail (*Setaria pumila*) with 7.9% average combined cover and Hairy crabgrass (*Digitaria sanguinalis*) with 2.6% average cover. The experiment did not contain weedy genera such as *Amaranthus*, *Bromus*, *Chenopodium*, *Cirsium*, *Daucus*, *Melilotus*, *Phalaris*, *Rumex*, or *Trifolium*, even though weeds of the genera *Bromus*, *Chenopodium*, *Cirsium*, *Melilotus*, *Rumex*, and *Trifolium* were found in the field surrounding our experiment and did not seem to pose a significant threat to prairie vegetation (T. L. Dickson and W. H. Busby 2004, The University of Kansas, personal observations). Still, further tests of our results are needed in large-scale sites with more aggressive weeds. Some weedy species may not have existed at our experimental site because the 40+ years of row-crop agriculture may have reduced their soil seed bank density (Buhler et al. 2001).

The treatment without grass seeds had a large amount of bare ground, largely because grasses produce more litter than forbs. Bare ground may lead to erosion from falling raindrops or water run-off (Ellison 1950), which is a major concern in many CRP sites (Jelinski & Kulakow 1996). Bare ground may also lead to increased establishment of weeds (Bergelson et al. 1993) and seeded species (Gross 1984). Therefore, in sites where erosion or weeds are potentially a problem, a nondominant cover species, such as *Schizachyrium scoparium* in eastern Kansas, should be planted along with prairie forbs if no other grasses are present. Even though bare ground was significantly higher in the no grass seed treatment than the other treatments, total aboveground biomass did not differ significantly. Forb species such as *H. maximiliani* and *C. fasciculata* had high enough biomass in 2004 to compensate for the absence of grass biomass.

Conclusions

We suggest that tallgrass prairie restorations, and possibly all grassland restorations, should be conducted similarly to Schramm's (1992) mosaic planting strategy. Part of the restoration should be seeded with most forb seed and little to no dominant grass seed (and possibly little to no dominant forb seed). The other part of the restoration should be seeded with the remaining forb seed and a low density of dominant grass seed. The spatial separation of forbs from grasses will likely maximize the establishment of expensive forb seeds because forbs in our study established best in the no grass treatment. If seeding two types of seed mix is too complicated, then dominant grass seed densities less than our low density should be used in all areas. Low grass density of 0.13, 0.01, and 0.08 g/m^2 of *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum nutans*, respectively, allowed for greater forb abundance and richness than high grass density and still allowed for good grass establishment ($1\ g/m^2 = 8.92$ pounds/acre; all weights in conclusions are pure live seed). Also, Dale and Smith (1986) found that sowing *A. gerardii*, *P. virgatum*, and *S. nutans* at 0.16, 0.03, and 0.08 g/m^2, respectively, ultimately led to the same grass cover in Arkansas as sowing at four times higher density.

Implications for Practice

- This study shows that the high seeding densities of dominant grasses common to many grassland restorations can decrease forb cover, biomass, and richness.
- High forb seeding densities can increase forb richness, even at high grass seeding densities, but high grass seeding densities appear to ultimately control forb cover and biomass.
- Forb seeding density should be maximized when high forb species richness and abundance is a restoration goal, but forb seed is generally much more expensive than grass seed. Therefore, it may be most economical to seed the majority of forb seed in areas with little to no dominant grass seed, thereby reducing competition from grasses and maximizing forb establishment. The remaining forb seed can be sown in areas with a low density of dominant grass seeds (probably no more than 1.9 pounds of live seed/acre).

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