Restoration of Prairie Community Structure and Ecosystem Function in an Abandoned Hayfield: A Sowing Experiment

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Abstract

Using a multispecies seed sowing experiment, we investigated the roles of seed and microsite limitation in constraining the restoration of native prairie diversity and ecosystem function in an abandoned upland hayfield in northeastern Kansas. Seeds of 32 native and naturalized plant species from the regional pool were sown into undisturbed and experimentally disturbed field plots. After six growing seasons, experimental sowing led to major shifts in species and functional group composition, increases in native species abundance and floristic quality, declines in abundance of non-native species, and increases in plant diversity. These changes in community structure led to significant changes at the ecosystem level including increases in light capture, peak biomass, primary production, litter biomass, root biomass, and C storage in roots. Our findings reveal the importance of seed limitations in constraining the natural recovery of prairie vegetation, biodiversity, and ecosystem functioning in this grassland and confirm broadcast sowing as a useful tool for the restoration of upland hayfield sites.

Key words: diversity, ecosystem function, hayfield, prairie restoration, seed limitation, succession, tallgrass prairie.

Introduction

Agricultural activity has all but eliminated the tallgrass prairies of North America (Samson & Knopf 1994; Robertson et al. 1997), resulting in a substantial reduction of biodiversity and ecosystem services in the central United States since the onset of European settlement (Mann 1986; Kindscher & Tieszen 1998; Polley et al. 2005; Kucharik et al. 2006). Efforts to restore native prairie on abandoned agricultural lands are now widespread. Many of these restorations have been carried out with the goal of restoring floristic diversity and native species composition. Other restorations, such as those carried out within the context of the conservation reserve program (CRP), are focused more on enhancing functional attributes of the ecosystem such as soil conservation, nutrient accumulation, primary production, and hydrological benefits (Burke et al. 1995; Baer et al. 2002; Kucharik et al. 2006). The potential of cultivated lands to act as a sink for atmospheric carbon (Fan et al. 1998) has fueled renewed interest in grassland restoration as a tool for carbon management (Metting et al. 2001; Baer et al. 2002; Kucharik et al. 2006). Given the potential role of biodiversity itself in regulating ecosystem function (Naeem et al. 1999; Tilman et al. 2001; Loreau et al. 2002), restorations conducted primarily to restore native floristic diversity should also result in benefits at the ecosystem level (Foster et al. 2004; Zobel et al. 2006) such as improved productivity and nutrient retention. Although prairie restorations on abandoned farmland are common in the central United States, only a few have been designed to adequately study the benefits of restoration to both plant community structure and ecosystem processes (Baer et al. 2002; Camill et al. 2004).

In this paper, we present plant community and ecosystem-level responses from a sowing experiment carried out in an abandoned hayfield located in northeast Kansas. Our study site is representative of successional old-fields that are highly abundant in the region and which have a history of tillage followed by use as cool-season hay or pasture (Jog et al. 2006). The developing vegetation on these abandoned sites is much less diverse than the native prairies that once occupied them prior to agricultural use (Kindscher & Tieszen 1998). The soils are eroded and depleted in organic matter and stocks of carbon (C) and nitrogen (N; Kindscher & Tieszen 1998). At our field site, native prairie plants are slowly invading upland portions of the field, presumably from seeds produced in remnant

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prairie adjacent to the site (Foster 2001). Despite some recolonization by native species after two decades of abandonment from hay production, the site at the start of this study was still largely dominated by introduced C_3 hay grasses: Smooth brome (*Bromus inermis*) and Tall fescue (*Lolium arundinaceum*) and a variety of non-native early successional species.

A general goal of our research at the site has been to understand factors that constrain rates of succession and which limit natural recovery of the dominant prairie vegetation, native diversity, and associated ecosystem functions on abandoned sites. Such an understanding is the first step in developing effective restoration strategies. Slow rates of colonization by prairie species into abandoned farmland could possibly be due to microsite limitations related to alterations of the soil environment imparted by prior management (altered resources or abiotic factors, extirpation of soil mutualists, etc.; Kindscher & Tieszen 1998; Bever et al. 2003; Murphy et al. 2004) and/or by strong competitive resistance to invasion imposed by the current dominant species. Limited dispersal could also constrain rates of reestablishment and interact with local mechanisms of invasion resistance to constrain rates of succession and ecosystem recovery. Dispersal limitations are likely acute in our area given the poor dispersal ability of many native prairie plants and the increasing isolation of native seed sources throughout the fragmented agricultural landscape. In this study, a multispecies sowing experiment has allowed us to (1) examine the extent to which natural conversion to prairie vegetation on abandoned hayfields is constrained by seed availability versus microsite limitation and (2) evaluate the utility of seed sowing in the restoration of abandoned hayfields. Processes that regulate succession or constrain the composition and diversity of a community should also have important consequences for ecosystem function (Odum 1969; Hobbie 1992; Chapin et al. 1997; Knops and Tilman 2000; Tilman et al. 2001). As a result, another goal of the project was to examine the ecosystem consequences of overcoming dispersal limitation in this system via multispecies sowing.

Our previous work has shown that for this abandoned hayfield, a one-time sowing of 32 species led to an increase in initial native plant establishment and diversity that was detectable in upland sites in early years of the study (Foster 2001; Foster et al. 2004). Here, we document the more profound impacts of sowing on community structure that have emerged on these uplands after six years and examine the consequences for ecosystem functioning. To evaluate the effectiveness of sowing for community restoration, we examine responses of species and functional guild composition, native species abundance, species and functional guild diversity, and a floristic quality index. To evaluate consequences at the ecosystem level, we examine responses of energy capture, standing crop biomass, annual net primary production (ANPP), litterfall, root biomass, and pool sizes of soil C and N. We discuss the results in

the context of successional mechanisms and community assembly and evaluate the relevance of our findings to the practice of restoration.

Methods

Study Site

This study was conducted at the Nelson Environmental Studies Area, a research facility managed by the Kansas Biological Survey at the University of Kansas and located within the prairie–forest ecotone region of northeastern Kansas (lat 39°03′N, long 95°12′W). The site used for this study is a 20-ha abandoned hayfield/pasture dominated by perennial grasses: Smooth brome (*Bromus inermis*, an introduced C_3 grass); Tall fescue (*Lolium arundinaceum*, an introduced C_3 grass); Kentucky bluegrass (*Poa pratensis*, an introduced C_3 grass); and Broomsedge (*Andropogon virginicus*, a native C_4 grass). The field, which had been historically plowed, has been undergoing secondary succession since abandonment in the early 1980s. In the two decades prior to abandonment, the site had been used for cool-season hay production but was also occasionally grazed by cattle. Since abandonment, the site has been periodically mown (every 3–4 years) to discourage shrub and tree invasion, although the site was not mown during the course of the present study 1999–2005. Fire has not been used as a management tool at our field site for at least 30 years. Soils are clay loam (montmorillonitic, mesic Aquic Argiudolls; U.S. Department of Agriculture Soil Conservation Service 1977). Plant productivity varies considerably across the site as a function of topography with the greatest productivity occurring in lowland swales along ephemeral drainages (Foster et al. 2004). The climate of the region is humid continental, with a mean annual temperature of 12.9°C and mean annual precipitation of 930 mm.

Experimental Design

In the fall of 1999, forty 2.5 × 2.5–m plots, each composed of four 1 × 1–m treatment quadrats, were distributed throughout the 20-ha field site (Foster 2001; Foster et al. 2004). In each plot, 1 × 1–m quadrats were separated by 0.5-m buffer strips. Plot locations within the field were selected using a stratified random method that assured adequate representation of upland and lowland communities. In this study, we present results from 17 plots situated on upland locations only. We excluded plots established in highly productive lowland swales because these communities represent fundamentally different assemblages from those for which we wished to make inferences—the upland grasslands which are ubiquitous in the region and which are an important target for restoration at our field station. As a result, this particular study presents data collected from a total of 68 upland quadrats (17 plots × 4 quadrats).

To each plot, a 2 × 2 factorial combination of treatments was assigned randomly to the four quadrats in each plot: two levels of multispecies sowing (seeds of 32 grassland species sown, seeds not sown); two levels of disturbance designed to remove biomass and alter microsite availability in the first four years of the experiment (disturbance, no disturbance). In 2000 and 2001, disturbances were applied by removing litter and raking the soil in January and then by clipping and removing the canopy to 15 cm height in April and June. In 2002 and 2003, the plots were clipped in April only and were not raked. In 2004 and 2005, all quadrats were left undisturbed.

Seeds for the experiment were purchased from two regional seed companies (Stock Seed Farms, Murdock, NE, U.S.A.; Delange Seed, Sedgwick, KS, U.S.A.). The seeds were sown evenly by hand into quadrats in January 2000 at a rate of 400 seeds per species. None of the seeds were scarified or otherwise pre-treated before sowing. Sown species represent a wide range of life history and functional groups present in the regional pool and contain both native prairie species (24) and naturalized grassland species (8; Table 1). Non-native species were sown to evaluate questions associated with the original objectives of the experiment (Foster 2001; Foster et al. 2004), which were not explicitly conceived to address the issues of prairie restoration addressed here. Two additional species, *L. arundinaceum* and *P. pratensis* (both introduced C_3 grasses) were also sown into the plots but are hereafter treated as non-sown species in this paper because both were already abundant in the majority of quadrats at the start of the study (Foster et al. 2002) and because their abundances were not increased by sowing. Treating these as non-sown species allows us to better evaluate the impact of adding novel species to the system.

At the start of the study, 14 of the 32 sown species were found to occur naturally within the 20-ha study site, whereas the remaining 18 species were found in nearby old-field and prairie habitats within 2 km of the study site (Foster 2001). Of the 14 species present within the immediate study area, two were found to be initially present at low abundance in a small number of the quadrats used for the present study. These species were *Rudbeckia hirta* (three quadrats) and *Monarda fistulosa* (one quadrat).

Measurements

In this paper, we present data on plant community and ecosystem responses gathered in the sixth year of the experiment. We harvested above-ground plant biomass from quadrats in mid-June and late September 2005 to capture peak biomass of most early- and late-season species. At each harvest, plant biomass was sampled in a quadrat by clipping the vegetation along the ground in a 0.1 × 1–m strip with electric grass shears. On each date, biomass was sorted to live and litter fractions, with live fractions further sorted to species. All plant materials were dried to constant mass in a forced-air oven set to

70°C. Immediately after the June harvest, root samples were extracted from all the quadrats in five randomly selected plots to estimate root biomass. Root cores were taken within the harvest strip locations of each quadrat using a 10-cm diameter × 20-cm deep soil auger. Root cores were soaked overnight in water and then rinsed over a screen the next day to remove soil. After drying to constant mass, root tissue was finely ground and analyzed for percent C and N content using a Carlo-Erba CN autoanalyzer.

Interception of photosynthetically active radiation (PAR interception) by the plant canopy was measured in each quadrat in early June and late September, just prior to the June and September biomass harvests using a PAR ceptometer probe (Decagon devices, Pullman, WA, U.S.A.). On each date, four measurements were taken above and below the canopy of each quadrat so that PAR interception could be expressed as a percentage of full sun [(1 − (PAR below canopy/PAR above canopy)) × 100]. PAR interception values for June and September were averaged before analysis.

Just prior to the June biomass harvest, two 2.5-cm diameter × 20-cm deep soil cores were taken from each quadrat to measure soil organic matter, soil carbon (C), and soil nitrogen (N). The two cores extracted from each quadrat were combined and then passed through a 2-mm sieve to remove root material. The samples were then air-dried before analysis. Percent soil C and N were determined using a LECO CN dry combustion analyzer. Percent soil organic matter was determined using the Walkley–Black procedure (Walkley & Black 1934).

Data Analysis

June and September biomass data were combined to evaluate species abundances, community composition, diversity, and primary production (ANPP). Species lists from both surveys were combined to capture both early- and late-season species. Peak biomass values for each species (biomass in June or September, whichever greater) were used to estimate individual species production and production of species aggregated by life history group, origin (native or non-native), and functional guild. Life history groups included annuals, short-lived perennials, and long-lived perennials. The functional guilds used were C_3 graminoids, C_4 graminoids, non-legume forbs, and legumes. Assignment of species to life history and functional guilds follows the U.S. Department of Agriculture, Natural Resources Conservation Service, Plant Database (http://plants.usda.gov/). We calculated four measures of plant diversity: species richness (*S*), Shannon diversity (*H'*; Magurran 1988), community evenness (*H'/H*$_{Max}$; Magurran 1988), and functional guild diversity (*H'*$_{FG}$). *H'*$_{FG}$ was calculated as Shannon diversity using biomass data aggregated by functional guild category. We also calculated Simpson's diversity, but because findings were no different, we report only the Shannon index. A floristic quality

Table 1. Species abundances in 2005 (quadrat occupancy and mean production: $g \cdot m^{-2} \cdot yr^{-1}$) in non-sown and sown quadrats.

Species	Life History/ Functional Guild[a]	CC	Origin[b]	Occupancy: Non-Sown Quadrats	Occupancy: Sown Quadrats	Production: Non-Sown Quadrats	Production: Sown Quadrats	Observed Indicator Value
Non-sown								
Acalypha virginica	AF	0	N	13	4	0.30	0.10	31**
Andropogon virginicus	C_4-PG	0	N	20	14	39.85	5.46	52**
Asclepias verticillata	PF	0	N	19	12	3.70	0.71	35**
Bromus inermis	C_3-PG	0	I	24	10	96.84	47.14	66**
Leptoloma cognatum	C_4-PG	0	N	16	3	17.60	3.82	43**
Lespedeza stipulacea	AL	0	I	9	1	0.80	0.01	23**
Lolium arundinaceum	C_4-PG	0	I	20	14	32.85	12.46	31**
Tridens flavus	C_4-PG	0	N	9	5	8.50	0.48	20*
Solidago canadensis	PF	0	N	11	5	19.10	2.85	21*
Sown								
Achillea millefolium	PF	1	N	—	1	—	<0.01	—
Amorpha canescens	PL	7	N	—	15	—	2.21	29**
An. gerardii	C_4-PG	4	N	1	24	0.15	84.1	70**
As. tuberosa	PF	6	N	—	5	—	0.015	6n.s.
Aster novae-angliae	PF	5	N	—	1	—	<0.01	—
Bouteloua curtipendula	C_4-PG	5	N	—	16	—	8.82	44**
<u>*Chrysanthemum leucanthemum*</u>	PF	0	I	—	—	—	—	—
Dactylis glomerata	C_3-PG	0	I	—	1	—	<0.01	3n.s.
Desmanthus illinoensis	PL	2	N	1	13	0.01	12.41	35**
Dalea candidum	PF	7	N	—	4	—	0.16	12n.s.
Dal. purpurea	PF	7	N	—	3	—	0.07	9n.s.
Echinacea pallida	PF	7	N	—	13	—	0.32	26**
Elymus canadensis	C_3-PG	5	N	—	3	—	0.64	9n.s.
<u>*Eragrostis trichodes*</u>	C_3-PG	4	N	—	—	—	—	—
<u>*Festuca ovina*</u>	C_3-PG	0	I	—	—	—	—	—
Les. capitata	PL	5	N	1	33	<0.01	247.24	94**
<u>*Liatris pycnostachya*</u>	PF	7	N	—	—	—	—	—
<u>*Medicago sativa*</u>	AL	0	I	—	—	—	—	—
<u>*Melilotus officinalis*</u>	BL	0	I	—	—	—	—	—
Monarda fistulosa	PF	3	N	—	17	—	7.45	32**
Panicum virgatum	C_4-PG	4	N	—	18	—	42.48	50**
<u>*Phleum pratense*</u>	C_3-PG	0	I	—	—	—	—	—
Ratibida columnifera	PF	4	N	—	6	—	1.10	15n.s.
R. pinnata	PF	3	N	—	2	—	<0.01	7n.s.
Rudbeckia hirta	PF	3	N	—	2	—	0.19	6n.s.
Salvia azurea	PF	4	N	—	29	—	27.47	79**
Schizachyrium scoparium	C_4-PG	5	N	1	30	2.35	49.55	69**
Sorghastrum nutans	C_4-PG	5	N	1	33	1.16	80.62	85**
Sporobolus cryptandrus	C_4-PG	0	N	6	22	1.85	15.36	58**
<u>*Trifolium pratense*</u>	PL	0	I	—	—	—	—	—
<u>*T. repens*</u>	PL	0	I	—	—	—	—	—
Tripsacum dactyloides	C_4-PG	3	N	—	22	—	191.75	52**

The only non-sown species shown are those that were found to be significant indicator species. All 32 sown species are listed, including nine (underlined species) that were absent from all quadrats in 2005.
[a] Life history/functional guilds: AF, annual forb; AL, annual legume; BL, biennial legume; PF, perennial forb; PL, perennial legume; C_3-PG, C_3 perennial grass; C_4-PG, C_4 perennial grass.
[b] N, native origin; I, introduced.
* $p < 0.05$; ** $p < 0.01$; n.s., not significant at $p > 0.05$.

index was calculated for each plot based on coefficients of conservatism (CC) assigned to native species in the region by Freeman and Morse (2002). CC values range from 0 to 10 with large values indicative of high-quality prairie species of narrow ecological niche and late-successional status. Smaller CC values indicate more widespread native species of earlier successional stages. A value of 0 was given to all non-native species. For each plot, we report

the modified floristic quality index of Rooney and Rogers (2002), which is simply the mean value of CC (Mean C) across all species present in a given community. We also calculated floristic quality using several other formulations (Freeman & Morse 2002) but report only one because all formulations yielded similar results.

ANPP was estimated by summing the peak biomass values for all species within a quadrat. This measure of

ANPP underestimates total annual production because it does not account for root growth and biomass losses resulting from consumption or tissue senescence. However, this measure accounts for a greater proportion of ANPP than a single biomass harvest conducted at peak standing crop.

We used two-factor, within-subjects analysis of variance (ANOVA) to examine the effects of disturbance and sowing on the production of species groups, measures of diversity, floristic quality, and ecosystem variables. To alleviate problems with heteroscedasticity, log transformations were applied to all biomass data and to the diversity indexes (H' and H'_{FG}). Square root and arcsine square root transformations were applied to species richness and light interception data, respectively, to correct for problems with nonnormality and heteroscedasticity. Parametric ANOVA could not be used to evaluate treatment effects on the biomass of some species groups because their data distributions could not be corrected via transformation to meet assumptions of ANOVA. In these cases, we used the nonparametric Scheirer–Ray–Hare test.

We used nonmetric multidimensional scaling (NMDS) as an ordination method to display variation in species and functional guild composition among quadrats. The nonparametric multiple response permutation procedure (MRPP; Zimmerman et al. 1985), operating on Euclidean distances, was used to evaluate the significance of disturbance and sowing effects on community composition. MRPP generates a chance-corrected within-group agreement value (A) which evaluates the level of within treatment homogeneity of species composition (McCune & Metford 1999). Indicator species analysis (ISA) was then applied to identify those species that contributed significantly to community-level divergence among treatments (Dufrene & Legendre 1997). The indicator value (IV) can range from 0 to 100. Perfect indication of a given treatment (IV = 100) occurs when a species is present in all replicates of only that treatment.

Univariate statistical analyses were performed using SPSS (version 12.0). Multivariate procedures were performed using PC ORD (version 4.14). Nomenclature follows Kartez and Meacham (2005).

Results

Community Composition and Floristic Quality

Of the 32 species sown, 23 were recorded in at least one quadrat in 2005 (Table 1). Of the 324 sown species occurrences in 2005, all but 11 were in sown quadrats. The production of sown species in aggregate was increased significantly by sowing, whereas the production of non-sown species was significantly decreased by sowing (Table 2). In the non-sown plots, sown species accounted for less than 2% of total production on average. In sown plots, sown species accounted for over 87% of total production. The production of annuals and short-lived perennials was significantly decreased by sowing, whereas that of long-lived perennials was significantly increased by sowing (Table 2). The production of native species was significantly increased by sowing, whereas that of non-native species was significantly decreased by sowing. The production of C_3 graminoids was significantly decreased by sowing, whereas that of C_4 graminoids and legumes was significantly increased by sowing.

As evaluated using MRPP, sowing significantly altered species composition ($A = 0.18$, $p < 0.0001$). This clear

Table 2. Treatment effects on the mean production ($g \cdot m^{-2} \cdot yr^{-1}$) of species grouped by sowing status, life history, origin, and functional guild.

Species/Species Group	−Seeds −Disturbance	+Seeds −Disturbance	−Seeds +Disturbance	+Seeds +Disturbance	Significant Factors
Sown/non-sown					
Sown species[a]	7.80	910.32	3.60	793.34	Sow***
Non-sown species	293.73	140.80	300.10	115.31	Sow***
Life history					
Annuals[a]	3.82	0.10	1.60	0.24	Sow***
Short-lived perennials	23.10	4.22	56.90	3.23	Sow**
Long-lived perennials	274.01	1,046.90	245.33	905.20	Sow***
Origin					
Native species	118.10	925.52	129.76	813.42	Sow***
Non-native species	183.33	125.62	174.40	95.22	Sow***
Functional guilds					
C_3 graminoids	182.93	127.01	198.71	97.43	Sow***
C_4 graminoids	81.11	614.80	64.70	502.10	Sow***
Non-legume forbs	36.33	42.22	39.32	48.20	n.s.
Legumes[a]	0.10	267.10	0.10	258.80	Sow***

When calculating biomass production of species grouped as either non-sown or sown, we treated the sown species, *Lolium arundinaceum* and *Poa pratensis*, as non-sown species in the formulation of these groups. See the Methods section for explanation.
[a] Nonparametric Scheirer–Ray–Hare test used in lieu of ANOVA.
** $p < 0.01$; *** $p < 0.001$; n.s., not significant at $p > 0.05$.

sowing effect is readily apparent from the complete separation of non-sown and sown quadrats along axis 1 of the NMDS ordination (Fig. 1A). ISA identified 22 species as significant indicators of the sowing effect on community composition (Table 1). All the non-sown indicator species (nine) were reduced in abundance by sowing. The sown indicator species (13), all of which were native, were increased in abundance by sowing. MRPP also revealed a marginally significant influence of disturbance on species composition ($A = 0.029$, $p = 0.053$). Quadrat scatter along axis 2 of the ordination suggested that sown quadrats responded more clearly to disturbance than non-sown plots. To test this possibility, we conducted MRPP to evaluate the effect of disturbance on species composition for sown and non-sown quadrats separately. We found that disturbance altered species composition significantly only among sown quadrats ($A = 0.042$, $p < 0.01$), suggesting a subtle interaction effect on species composition. As indicated by ISA, the disturbance effect in sown plots primar-

ily reflects a contrast in production between the sown C_4 grass *Tripsacum dactyloides* (IV = 61.8, $p < 0.01$), which was reduced in production by disturbance and three other sown C_4 grasses that were all increased in production by disturbance: *Panicum virgatum* (IV = 58.7, $p < 0.05$), *Sorghastrum nutans* (IV = 63.5, $p < 0.05$), and *Schizachyrium scoparium* (IV = 60.0, $p < 0.05$).

Not surprisingly, sowing also significantly altered functional guild composition ($A = 0.18$, $p < 0.0001$) as is apparent in the NMDS ordination of functional guild composition (Fig. 1B). This sowing effect reflects a contrast between the C_3 grasses (IV = 63.0, $p < 0.01$), which were reduced in production by sowing and the C_4 grasses (IV = 88.5, $p < 0.01$) and legumes (IV = 99.7, $p < 0.01$), which were increased in production by sowing. Disturbance had no impact on functional guild composition ($A = 0.009$, $p > 0.05$).

Floristic quality measured as Mean C was significantly increased by sowing but was unaffected by disturbance (Fig. 2). Values ranged between 0 and 3.2 for non-sown plots and between 2.7 and 4.8 for sown plots.
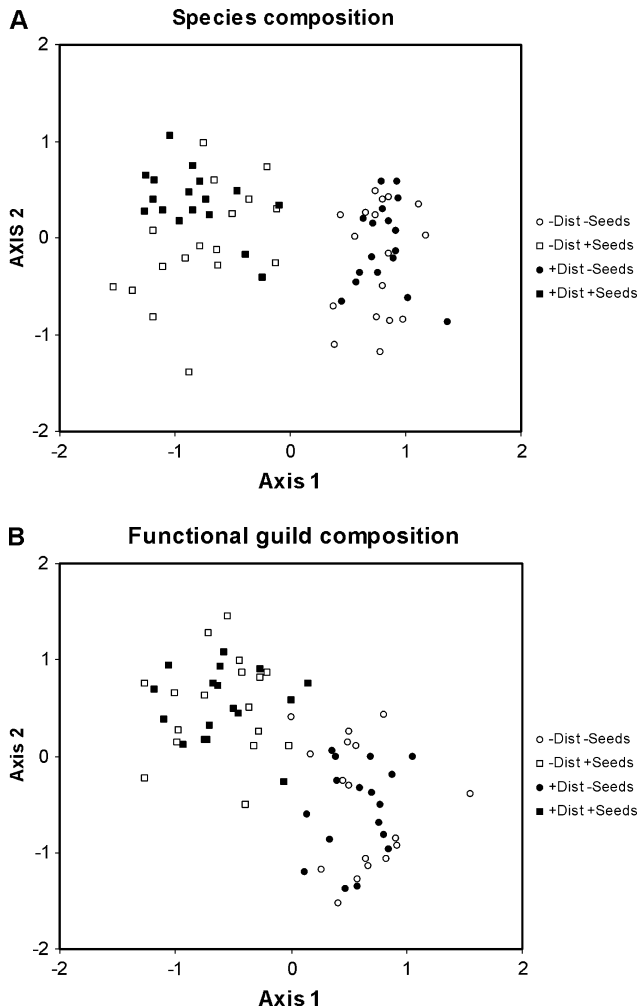
Diversity

The mean richness of sown species was significantly increased by sowing (Table 3) but to a greater extent in disturbed than in nondisturbed quadrats (sowing × disturbance interaction). The mean richness of non-sown, resident species was significantly reduced by sowing. Mean total species richness and mean Shannon diversity were both increased significantly and additively by sowing and disturbance, although the magnitude of the sowing effect was greater than the disturbance effect (Table 3). Mean community evenness and functional guild diversity were both increased significantly by sowing.

Ecosystem Responses

Litter mass was significantly increased by sowing and disturbance. However, the positive effect of sowing on litter

Figure 1. NMDS ordinations of (A) species and (B) functional guild composition.
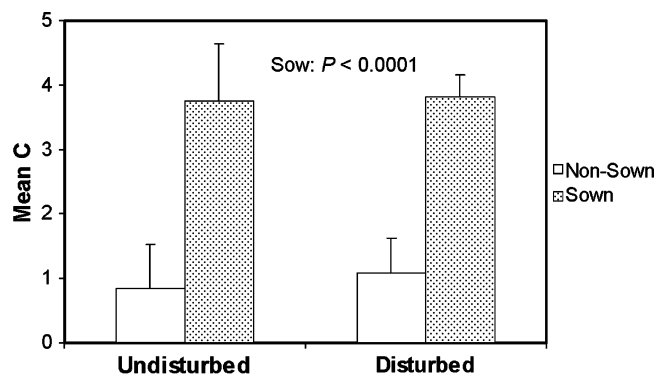
Figure 2. Response ($\bar{X} + 1$ SD) of floristic quality (Mean C) to sowing and disturbance.

Table 3. Treatment; effects on measures of plant diversity.

Diversity Measure	−Seeds −Disturbance	+Seeds −Disturbance	−Seeds +Disturbance	+Seeds +Disturbance	Significant Factors
Sown species richness[a]	0.41	8.01	0.42	10.05	Sow**, Dist*, Sow × Dist**
Non-sown species richness	7.12	4.58	8.05	5.01	Sow***
Total species richness (S)	7.53	12.60	8.50	15.10	Sow***, Dist***
Species diversity (H'_{SP})	1.15	1.56	1.32	1.85	Sow***, Dist**
Community evenness (H'/H_{Max})	0.56	0.65	0.59	0.72	Sow**
Functional diversity (H'_{FG})	0.53	0.89	0.67	0.98	Sow***

[a] Nonparametric Scheirer–Ray–Hare test used in lieu of ANOVA.
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

was of greater magnitude in disturbed than in nondisturbed plots (sowing × disturbance interaction; Table 4). Root biomass, peak above-ground biomass, ANPP, and PAR interception were all significantly increased by sowing (Table 4). On average, sowing increased mean peak biomass by a factor of 3.3, mean ANPP by a factor of 3.2, and mean root biomass by a factor of 2.7. Carbon storage in roots and root tissue C:N ratio both were increased significantly by sowing. Soil organic matter and percent soil C and N were unaffected by sowing and disturbance.

Discussion

After six growing seasons, experimental sowing led to shifts in species and functional group composition, increases in native species abundance and floristic quality, declines in abundance of non-native species, and increases in plant diversity. These shifts in community structure led to changes at the ecosystem level including increases in light capture, peak biomass, primary production, litter biomass, root biomass, and C storage in roots. Our findings reveal the importance of seed limitations in constraining the natural recovery of prairie vegetation, biodiversity, and ecosystem functioning in this grassland and confirm sowing as a useful tool for the restoration of upland hayfield sites.

Community Responses

An assessment of recent sowing experiments suggests that seed limitations of plant diversity and composition may be common in plant communities, particularly those that support low to moderate levels of productivity (Tilman 1997; Zobel et al. 2000; Foster 2001; Foster & Tilman 2003; Eskelinen & Virtanen 2005; Houseman & Gross 2006; Zeiter et al. 2006). However, as suggested by Zobel and Kalamees (2005), the role of seed limitation in plant communities may often be overestimated due to the short duration of most of these experiments. Diversity enhancement in response to sowing in short-term experiments could be overly influenced by the initial responses of seedlings and juveniles, responses that could turn out to be transient and thus inconsequential to the community over the long term. In our study, sowing led to unambiguous changes in plant composition, floristic quality, and diversity. After six years, native species, particularly native C_4 grasses and legumes, dominated the sown plots, comprising 89% of community production. Sowing also reduced the biomass of non-sown resident species by an average of 57%, reflecting rapid competitive decline in the abundance of resident annual and short-lived perennial species and resulting in the average local extinction of 2.8 non-sown species per quadrat. Sowing increased floristic quality to similar levels recorded in nearby native prairies used for hay or grazing (Jog et al. 2006).

Table 4. Treatment effects on ecosystem variables.

Ecosystem Variable	−Seeds −Disturbance	+Seeds −Disturbance	−Seeds +Disturbance	+Seeds +Disturbance	Significant Factors
Litter mass (g/m^2)	221.02	482.82	280.63	699.40	Sow**, Dist**, Sow × Dist*
Root mass (g/m^3)	233.86	778.29	203.04	411.18	Sow*
Peak biomass (g/m^2)	269.02	969.41	276.40	822.85	Sow***
ANPP (g·m^{-2}·yr^{-1})	301.47	1,051.14	303.80	908.64	Sow***
PAR interception (%)	80.65	92.80	82.76	95.82	Sow***
C storage in roots (g/m^3)	83.58	291.44	72.96	150.70	Sow*
N storage in roots (g/m^3)	4.04	10.82	3.58	5.54	n.s.
Root C:N	20.54	35.10	19.16	29.65	Sow**
Soil organic content (%)	3.22	2.99	2.97	3.09	n.s.
Total soil C (%)	1.95	1.81	1.84	1.86	n.s.
Total soil N (%)	0.17	0.16	0.16	0.16	n.s.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s., not significant at $p > 0.05$.

It is clear that the decline in abundance of non-sown species in our sown plots was the result of removing dispersal barriers of superior competitors in the regional pool, particularly the native C_4 grasses, which rose from initial rarity at the time of sowing to eventual dominance. These native perennial grasses are known to be efficient competitors for N (Tilman & Wedin 1991), a resource that is limiting at our field site (Kincaid et al. 2002; Billings et al. 2006).

These findings indicate that diversity and the dominant species composition of plant neighborhoods are strongly constrained by dispersal limitation in this grassland and that microsite limitation is of secondary importance. Microsite limitation was implicated by positive effects of experimental disturbance on sown species richness, total richness, and Shannon diversity. Disturbance also altered community composition, but only in sown quadrats, illustrating an interaction between species availability and disturbance on community structure. It appears that the subtle disturbance effect on species composition observed in sown quadrats resulted entirely from differential responses to disturbance among sown species in the same functional guild: the C_4 graminoids. This explains why there was no effect of disturbance on functional guild composition. The sown C_4 grass, *Tripsacum dactyloides*, established and performed much better in undisturbed quadrats than the other sown C_4 grasses which have much smaller seeds. It is not clear why this occurred, but it may reflect the advantage that big seeds give to *Tripsacum* in establishing in thick litter and undisturbed vegetation. Although the above responses to experimental disturbance implicate microsite limitation, seed limitation appears to be of much greater significance to the community.

Our results show that these grasslands, once released from intensive management (annual haying and fertilization), become highly invasible and unstable systems that convert rapidly (<6 years) to dominance by late-successional prairie species in the absence of seed limitations. The extreme degree to which succession is constrained in these systems by seed availability is illustrated by the fact that all the sown species that are currently abundant in sown quadrats have source populations within 200 m, yet have failed to colonize and dominate on their own after more than 20 years of abandonment.

In the absence of mowing or burning, abandoned agricultural fields will eventually succeed to shrub and tree dominance in our region (Fitch & Kettle 1988; Cook et al. 2005). However, the speed of this conversion depends to a large extent on the distance of a locality from sources of woody plant propagules (Yao et al. 1999; Cook et al. 2005). In a long-term, permanent plot study of old-field succession conducted nearby in the absence of disturbance (Cook et al. 2005), prairie plants were virtually absent from the herb-dominated stages of succession (1–14 years postabandonment) before woody plants rose to dominance. The herb stage was instead dominated primarily by well-dispersed broadleaf forbs in the Asteraceae: *Solidago canadensis* and various species in the genus *Aster*. Our findings in the current study suggest that the lack of a period of dominance by the native tallgrasses and other prairie species during old-field succession is largely the result of seed limitation rather than microsite limitation.

Although our study supports strong seed limitation of diversity, the dominant prairie tallgrasses, and of several other prairie species, it is important to note that many prairie species may be limited by other factors. Of the 24 prairie species sown in this experiment, two were absent from the community by the sixth-growing season and only 11 of the remaining 22 were present in plots as abundant reproductive adults. It is possible that local microsite availability or biotic limitations such as resource competition, seed predation, a lack of soil mutualists (Bever et al. 2003), or the presence of natural enemies may be more important constraints for these species than seed limitation.

Ecosystem Responses

In this study, seed additions led to substantial changes in a number of ecosystem characteristics, indicating that seed availability can limit the recovery of community structure and ecosystem functioning during succession on these abandoned hayfields. The positive effect of sowing on productivity observed here largely reflects the successful establishment and growth of native C_4 grasses. However, the most abundant species in sown quadrats was a common prairie legume, *Lespedeza capitata*, which likely enhanced the productivity of sown quadrats even further via nitrogen fixation. These observed impacts of sowing on productivity suggest that even 20 or more years after abandonment, productivity of abandoned hayfields may be far below their potential maximum as a result of dispersal limitations. As a point of comparison, mean peak above-ground biomass in the sown quadrats of this experiment (895 g/m^2) exceeded the long-term average recorded in nearby native prairie on the same soil type (718 g/m^2; Kettle et al. in preparation), suggesting that ANPP can be restored rapidly upon release from dispersal constraints as accomplished in this study through sowing. These results are consistent with studies showing that the productivity of prairie restorations can equal or even exceed that of nearby native prairie (Baer et al. 2002; Martin et al. 2005). Productivity in restorations may be greater than in undisturbed prairie due to residual nitrogen in soil from agricultural uses at the time of abandonment or from the use of highly productive grass cultivars (Knapp & Dyer 1998; Baer et al. 2002). The presence of sown legumes, at much higher abundances than in nearby native prairie, may partially explain the greater productivity of sown quadrats in our study.

Although sowing led to rapid recovery of productivity, and thus C capture by the ecosystem, there was no similar recovery of soil organic matter or total C and N content. This is not unexpected given that organic matter typically accumulates very slowly in soils abandoned from agriculture (Knops & Tilman 2000). Baer et al. (2002) found that total soil C and N increased only very slightly across a 12-year

chronosequence of abandoned fields that had been planted to native C_4 grasses as part of the CRP. This and other studies (Burke et al. 1995; Knops & Tilman 2000) indicate that it would likely take many decades or even centuries to recover pre-agricultural levels of soil organic matter on abandoned old-fields and/or prairie restorations (Kindscher & Tieszen 1998). In our study, we do expect to eventually see increased organic matter and soil C in our sown quadrats given their drastically altered composition and enhanced productivity. We did find greater storage of C in roots in the sown quadrats, reflecting greater root biomass and higher C content (higher C:N ratio) of root tissue. Over time, these differences are expected to lead to greater long-term C storage in soil organic matter (Baer et al. 2002).

Conclusions: Implications for Succession and Restoration

Although numerous mechanisms regulate secondary succession, dispersal limitations clearly play a large role in governing rates of community change following abandonment (Pickett et al. 1987; Myster & Pickett 1993; Tilman 1994; Foster & Gross 1999; Cook et al. 2005). Our results show that early successional species including annuals, short-lived perennials, and introduced C_3 grasses originally planted for hay can persist for many years after abandonment. However, this persistence is unstable, transient and reflects slow arrival of superior native competitors that can rapidly replace early successional species once severe dispersal limitations are overcome. Our findings generally support the competition–colonization trade-off as a fundamental mechanism driving rates of secondary succession on abandoned agricultural lands (Tilman 1994; Pacala & Rees 1998).

As landscapes become more fragmented and native species pools become further diminished, rates of vegetation recovery following land abandonment will likely degrade further as a result of acute seed limitation, with important consequences for recovery of ecosystem functions. Our findings indicate that the sowing of abandoned upland sites in our region may be effective to assist vegetation recovery and enhance many aspects of community structure and function including native species composition, native diversity, ANPP, and some components of soil function and nutrient cycling.

Implications for Practice

- On abandoned cool-season hayfields in the Midwest, seed limitation can strongly limit rates of natural succession toward prairie and, as a result, limit the recovery of primary production and other ecosystem-level processes.
- By circumventing seed limitations, broadcast sowing can be an affective tool for prairie restoration of abandoned cool-season grasslands, with positive benefits at the ecosystem level.

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