Effects of hay management and native species sowing on grassland community structure, biomass, and restoration

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Abstract. Prairie hay meadows are important reservoirs of grassland biodiversity in the tallgrass prairie regions of the central United States and are the object of increasing attention for conservation and restoration. In addition, there is growing interest in the potential use of such low-input, high-diversity (LIHD) native grasslands for biofuel production. The uplands of eastern Kansas, USA, which prior to European settlement were dominated by tallgrass prairie, are currently utilized for intensive agriculture or exist in a state of abandonment from agriculture. The dominant grasslands in the region are currently high-input, low-diversity (HILD) hay fields seeded to introduced C_3 hay grasses. We present results from a long-term experiment conducted in a recently abandoned HILD hay field in eastern Kansas to evaluate effects of fertilization, haying, and native species sowing on community dynamics, biomass, and potential for restoration to native LIHD hay meadow.

Fertilized plots maintained dominance by introduced grasses, maintained low diversity, and were largely resistant to colonization throughout the study. Non-fertilized plots exhibited rapid successional turnover, increased diversity, and increased abundance of C_4 grasses over time. Haying led to modest changes in species composition and lessened the negative impact of fertilization on diversity. In non-fertilized plots, sowing increased representation by native species and increased diversity, successional turnover, and biomass production. Our results support the shifting limitations hypothesis of community organization and highlight the importance of species pools and seed limitations in constraining successional turnover, community structure, and ecosystem productivity under conditions of low fertility. Our findings also indicate that several biological and functional aspects of LIHD hay meadows can be restored from abandoned HILD hay fields by ceasing fertilization and reintroducing native species through sowing. Declines in primary production and hay yield that result from the cessation of fertilization may be at least partially compensated for by restoration.

Key words: biofuel; biomass; diversity; hay management; HILD grassland; LIHD grassland; native hay meadows; productivity; restoration.

INTRODUCTION

In recent years, the potential benefits of native tallgrass prairie vegetation has been increasingly recognized by conservationists, private landowners, and the general public in terms of conservation value for biodiversity, wildlife habitat, soil protection, and a range of other ecosystem services and aesthetic values (Baer et al. 2002, Tunnell 2004, Polley et al. 2005, Foster et al. 2007). In addition, there is growing interest in the potential use of low-input, high-diversity (LIHD) grasslands, such as tallgrass prairie or prairie hay meadows for biofuel production (Tilman et al. 2006, Wallace and Palmer 2007, Fargione et al. 2008). While LIHD grasslands may yield less biofuel per hectare than high input, low diversity (HILD) crops such as corn, LIHD systems have much lower input costs while providing additional benefits and ecosystem services as

described above and can be utilized on marginal lands (Hill et al. 2006, Wallace and Palmer 2007).

In the central United States, native prairie hay meadows are important reservoirs of biodiversity in the former tallgrass prairie region and are the object of increasing attention for conservation and restoration (Kindscher et al. 2005, Jog et al. 2006). A great deal of research has been conducted on the biodiversity, conservation and restoration of hay meadow systems in Europe (Smith et al. 2000, Jefferson 2005, Knop et al. 2006, Marini et al. 2008). In contrast, very little research has been conducted for native hay meadows of the tallgrass prairie region. This discrepancy may in part be due to the paucity of policy in the United States to protect biodiversity in agricultural landscapes.

In the current agricultural landscapes of eastern Kansas (USA) where our studies are focused, privately owned native hay meadows, dominated by warm-season (C_4) grasses, are the most significant repository of prairie species, despite occupying less than 1% of the total land area (Kindscher 2005, Jog et al. 2006). The

high diversity of native hay meadows partially results from the fact that they have never been plowed and are seldom fertilized. In eastern Kansas, native hay meadows are hayed once per a year in mid-late summer, providing quality forage when managed cool-season hay fields are dormant. Annual haying disturbance works well to maintain diversity in a system historically regulated by nomadic grazers and fire (Shortridge 1973, Kindscher 2005).

Most of the upland landscape in this region, which was historically dominated by diverse tallgrass prairie vegetation, is currently utilized for intensive agriculture or has been abandoned from such use (Kettle et al. 2000). Much of this land is currently dominated by managed cool-season grasslands, occupying several million acres (Moyer and Sweeney 1988, Price et al. 2002, Guo et al. 2003, Kindscher 2005). These grasslands are typically HILD hay fields seeded to introduced C_3 grass cultivars (*Bromus inermis* and/or *Lolium arundenaceum*) on formerly tilled lands or sites recently abandoned from such use. Inputs to HILD grasslands include annual fertilization, particularly with nitrogen and phosphorus, to maintain high levels of production and forage quality much earlier in the summer (May–June) than can be achieved on native LIHD hay meadows dominated by warm-season grasses (Moyer and Sweeney 1988, Lamond et al. 1992, Henning et al. 1993). Other inputs to HILD hay fields include occasional applications of lime and broadleaf herbicides (Lamond et al. 1992).

Although efforts are in place to preserve remaining native hay meadows and their associated ecosystem benefits, their rarity in the landscape necessitates restoration if these benefits are to be expanded. As the cost of fertilizers increase and as the potential for utilizing native vegetation for conservation, ecosystem services, and biofuel production is realized, land owners may consider converting HILD hay fields, or lands abandoned from such use, to restored LIHD hay meadows. However, there is little data on how HILD and LIHD compare on similar sites or how to best restore HILD to LIHD systems. While HILD systems are maintained by inputs of nutrients, conversion to LIHD will require cessation of these inputs and possibly enhancement of native propagule pools because the recruitment of native species from the seed bank is likely to be limited.

In this paper, we present data from a long-term experiment conducted in a recently abandoned HILD hay field to evaluate responses of plant community structure and biomass yield to hay production management and native species restoration in eastern Kansas. Hay management is similar to potential biofuel management in that aboveground biomass is removed annually from the system. We evaluate the effects of fertilization on plant community structure and biomass and assess how these effects may be modified by annual haying. A native seed addition treatment allows us to (1) test the extent to which community dynamics, the natural reestablishment of native prairie species, and biomass production are constrained by propagule availability and (2) to examine the feasibility of reestablishing native vegetation via restorative sowing under varying conditions of fertilization and haying management.

To best understand the results and their implication for community and ecosystem restoration, we interpret our findings in light of a basic conceptual model of plant community organization, the shifting limitations hypothesis (SLH; Foster et al. 2004). Like the models of Grime (1979), Huston (1979, 1994), and Kondoh (2000), the SLH evaluates the interaction of habitat productivity and disturbance in regulating colonization and diversity in communities. However, the SLH also incorporates the potential role of dispersal limitation and species pools as constraints to colonization and coexistence at varying levels of soil fertility or productivity. The SLH predicts that the extent to which dispersal limitation vs. niche availability constrains community dynamics and diversity will change along gradients of soil fertility and productivity. Dispersal limitation and species pools are predicted to be most limiting at low to moderate productivity, but decline in importance at high productivity due to the increasing role of competitive exclusion. As predicted by Huston (1994, 1999), Grime (1979), and Kondoh (2000), the SLH also predicts that moderate disturbances occurring at high fertility and high potential productivity will increase diversity by increasing resource availability, reducing competitive dominance, and allowing a greater proportion of the available species pool to colonize and persist under conditions that would otherwise lead to exclusion. In the context of our study, the SLH predicts (1) that sowing native prairie species will increase colonization rates, accelerate successional change and native species accumulation, increase diversity, and alter species composition to the greatest extent in non-fertilized plots; (2) that haying should increase plant colonization rate and diversity at high fertility by interrupting competitive exclusion; and (3) as follows from prediction 2, sowing will have a stronger impact on diversity and composition in fertilized plots if they have also been hayed.

A final objective of the study was to examine effects of fertilization, haying, and sowing on biomass production and potential hay yield. Although fertilization maintains yields in HILD hay fields, there are several potential costs to annual applications of fertilizers and other inputs beyond the monetary, including export of pollutants to groundwater, soil acidification, increased greenhouse gas emissions (N_2O and CO_2; Billings et al. 2006), habitat homogenization, and biodiversity loss. Here we investigate the extent to which restorative sowing of native plants may affect biomass production and potentially compensate for reductions in production

resulting from the elimination of the fertilizer inputs typical to HILD management.

To summarize, the objectives of this study were to (1) evaluate effects of nutrient enrichment, annual haying, and their interaction on plant community dynamics, diversity, and biomass production and (2) examine the extent to which these effects are dependent upon species pools and dispersal limitations. In addressing these two objectives, we test the SLH in the context of hay meadow grasslands and evaluate constraints to the restoration of native LIHD hay meadows on lands currently utilized by, or recently abandoned from nonnative HILD hay production.

Methods

Study site

The study site is located in a former HILD, cool-season hay field at the University of Kansas Field Station and Ecological Reserves, a research unit of the Kansas Biological Survey and the University of Kansas. The Field Station is located within the deciduous forest–tallgrass prairie ecotone of eastern Kansas (Jefferson County; 39°03′ N, 95°12′ W). Soils are clay and silty loams formed from glacial deposits of loess over till. Mean annual precipitation is 900 mm with mean annual temperature of 13°C (Fitch and Kettle 1988).

The study site has had a long history of cultivation, but was utilized more recently as a cool-season (HILD) hay field until approximately 1987. The site was then maintained by periodic mowing until 1999, prior to the initiation of the current study. At the start of this study in 2000, the site was dominated by introduced C_3 grasses previously planted for hay: *Bromus inermis* and *Lolium arundinaceum*. Other grasses included *Poa pratensis* (introduced C_3 grass) and *Andropogon virginicus* (native C_4 grass). *Solidago canadensis*, *Eupatorium altissimum*, and *Asclepias syriaca* were common forbs species at the site at that start of the study.

Experimental design and setup

In March 2000, we established a 4×4 grid of 16 10×20 m plots at the site. Plots were separated by 3-m buffer strips. Each 10×20 m plot was divided into two contiguous 10×10 m subplots (yielding a total of 32 subplots). A $2 \times 2 \times 2$ factorial set of treatments was assigned to the experimental plots and subplots in a split-plot design: two levels of nutrient fertilization (fertilized; non-fertilized) applied as the whole-plot factor; two levels of native prairie seed sowing (seed of 41 species sown; non-sown) applied as a whole plot factor, and two levels of haying (hayed; non-hayed) applied as the split-plot factor. There are four replicates of each treatment combination.

NPK fertilizer (29-3-4) was spread by hand to each 10 $\times$ 20 m whole plot at a rate of 14–16 g N·m^{-2}·yr^{-1}. This application rate is at the high end of what is typically applied to production cool-season hay fields of the region (Moyer and Sweeney 1988, Lamond et al. 1992,

Henning et al. 1993). In 2000, 2001, and 2002, fertilizer was applied in two doses: 8 g N/m^2 in early April and 8 g N/m^2 in either late May or early June. In 2003–2007, one application of NPK at a rate of 14 g N/m^2 was applied in mid-April. From 2002 to 2006, one subplot in each whole plot was hayed annually in mid-late June as is typical for the cool-season hay fields of the region. Haying was accomplished by mowing the vegetation to near-ground level and removing thatch. In 2007, the last year of the study, haying was suspended so that yields for that year could be estimated for both June and early September instead of just in June.

Seeds of 41 native prairie species, common to prairie hay meadows, were sown by hand in eight of the 16 whole plots in February 2003 and 2004 at an average rate of 47 seeds/m^2 for each species. Sown species included the abundant prairie grasses and legumes of the region (Kettle and Whittemore 1991) and a variety of non-legume forbs (Table 1). At the start of the study, all sown species were found to be naturally present in a nearby remnant prairie. At this time, only three of the sown species were found to be naturally present at low abundance within the experimental plots. These species are *Eupatorium altissimum* (perennial forb), *Sorghastrum nutans* (C_4 perennial grass), and *Verbena stricta* (annual forb).

Vegetation sampling

In 2001–2006, we sampled aboveground standing crop biomass annually in the experimental subplots. Each year, samples were harvested in mid-June (June standing crop), just prior to haying when cool-season grasslands are at peak production. In the final year of this study (2007), a year in which we did not hay any of the subplots, we sampled standing crop biomass in June and in early September. Early September sampling was done to estimate peak-season biomass in unfertilized plots that had become dominated late in the study by warm-season grasses, which maximize growth later in the season (mid-August to early September) than C_3 grasses (Towne and Ohlenbusch 1992).

To sample biomass, two 0.1×2 m strips of aboveground plant material were harvested in each subplot with electric clippers. Biomass was clipped at ground level and all litter was collected. Samples were separated into live and litter fractions, with the live fraction further sorted to species. All fractions were dried to constant mass at 74°C in a forced-air oven and then weighed.

Data analysis

Species abundances.—We evaluated patterns of abundance over time and in response to experimental treatments for select species and species groupings. We evaluated biomass responses of the most abundant non-sown and sown species (all perennial grasses) and responses of species grouped as C_3 grasses, C_4 grasses, forbs, non-sown species, and sown species. Ideally,

TABLE 1. List of sown species, their functional guild, and their plot frequencies (percentage of plots occupied), in non-sown and sown plots under fertilized and non-fertilized conditions in the final year of the study (2007).

Species	Functional guild†	Not Sown		Sown	
		Non-fertilized	Fertilized	Non-fertilized	Fertilized
Achillea millefolium	PNLF	0	12.5	12.5	12.5
Agastache nepetoides	PNLF	0	0	0	0
Amorpha canescens	PLF	0	0	25	0
Andropogon gerardii	C_4-PG	0	0	100	12.5
Asclepias tuberosa	PNLF	0	0	37.5	0
Aster novae-angliae	PNLF	0	0	25	0
Astragalus canadensis	PLF	0	0	0	0
Bouteloua curtipendula	C_4-PG	0	0	62.5	0
Cassia chamaecrista	AF	0	0	25	0
Dalea candida	PLF	0	0	25	0
Dalea purpurea	PLF	0	0	12.5	0
Desmanthus illinoensis	PLF	0	0	87.5	25
Echinacea pallida	PNLF	0	0	62.5	0
Elymus canadensis	C_3-PG	0	0	25	0
Eragrostis trichodes	C_4-PG	0	0	0	0
Eryngium yuccifolium	PNLF	0	0	62.5	0
Eupatorium altissimum	PNLF	12.5	0	12.5	0
Festuca ovina	C_3-PG	0	0	0	0
Gentiana flavida	PNLF	0	0	0	0
Helianthus maximiliani	PNLF	0	0	87.5	12.5
Helianthus rigidus	PNLF	0	0	0	0
Heliopsis helianthoides	PNLF	0	0	87.5	12.5
Lespedeza capitata	PLF	0	0	100	0
Liatris pycnostachya	PNLF	0	0	12.5	0
Monarda fistulosa	PNLF	0	0	100	62.5
Oenothera missouriensis	PNLF	0	0	0	0
Panicum virgatum	C_4-PG	0	0	62.5	0
Penstemon albidus	PNLF	0	0	100	50
Ratibida columnifera	PNLF	0	0	100	2
Ratibida pinnata	PNLF	0	0	100	12.5
Rudbeckia hirta	PNLF	0	0	100	12.5
Salvia azurea	PNLF	0	0	100	5
Schizachyrium scoparium	C_4-PG	0	0	100	0
Silphium laciniatum	PNLF	0	0	25	0
Silphium perfoliatum	PNLF	0	0	37.5	0
Solidago rigida	PNLF	0	0	50	0
Sorghastrum nutans	C_4-PG	25	0	100	12.5
Sporobolus cryptandrus	C_4-PG	12.5	0	62.5	0
Teucrium canadense	PNLF	12.5	0	12.5	0
Verbena stricta	PNLF	12.5	0	50	0
Zizia aurea	PNLF	0	0	12.5	0

Notes: All taxonomic names are from the USDA Plants Database ⟨http://plants.usda.gov/⟩; $n = 8$ subplots for each treatment combination.

† Key to abbreviations: AF, annual forb; PLF, perennial leguminous forb; PNLF, perennial non-leguminous forb; C_3-PG, perennial grass with a C_3 photosynthetic pathway; C_4-PG, perennial grass with a C_4 photosynthetic pathway.

species abundance data would be analyzed using repeated measures ANOVA (RMANOVA). However, the data were highly heteroscedastic and could not be suitably transformed for parametric analysis. As a result, we qualitatively evaluated species abundance trends (means) across the entire run of years.

Plant diversity and biomass production.—A factorial RMANOVA was used to examine treatment effects on plant diversity and biomass yield measured as aboveground standing crop sampled in June each year. Year and haying are within-subjects factors. Fertilization and sowing are between-subjects factors. Diversity was evaluated as richness (S, number of species in a sample) and Shannon diversity index (H'; Magurran 1988). For 2007 only, we used within-subjects ANOVA to examine treatment effects on peak-season standing crop. Peak-

season standing crop is our best estimate of maximum biomass production toward the end of the study when non-fertilized and fertilized plots had diverged in species composition. In 2007, the seasonal peak for the C_3-dominated, fertilized plots and the C_4-dominated, non-fertilized plots occurred in June and September, respectively.

Community ordination.—To examine patterns of plant community variation within the experiment in the final year of the study (2007), we used nonmetric multidimensional scaling (NMDS) to produce an ordination of subplots based on biomass of all species recorded in the June biomass harvests. To better visualize effects of sowing on community composition at low and high fertility separately, we partitioned the ordination by fertilization level. We used the nonparametric multiple
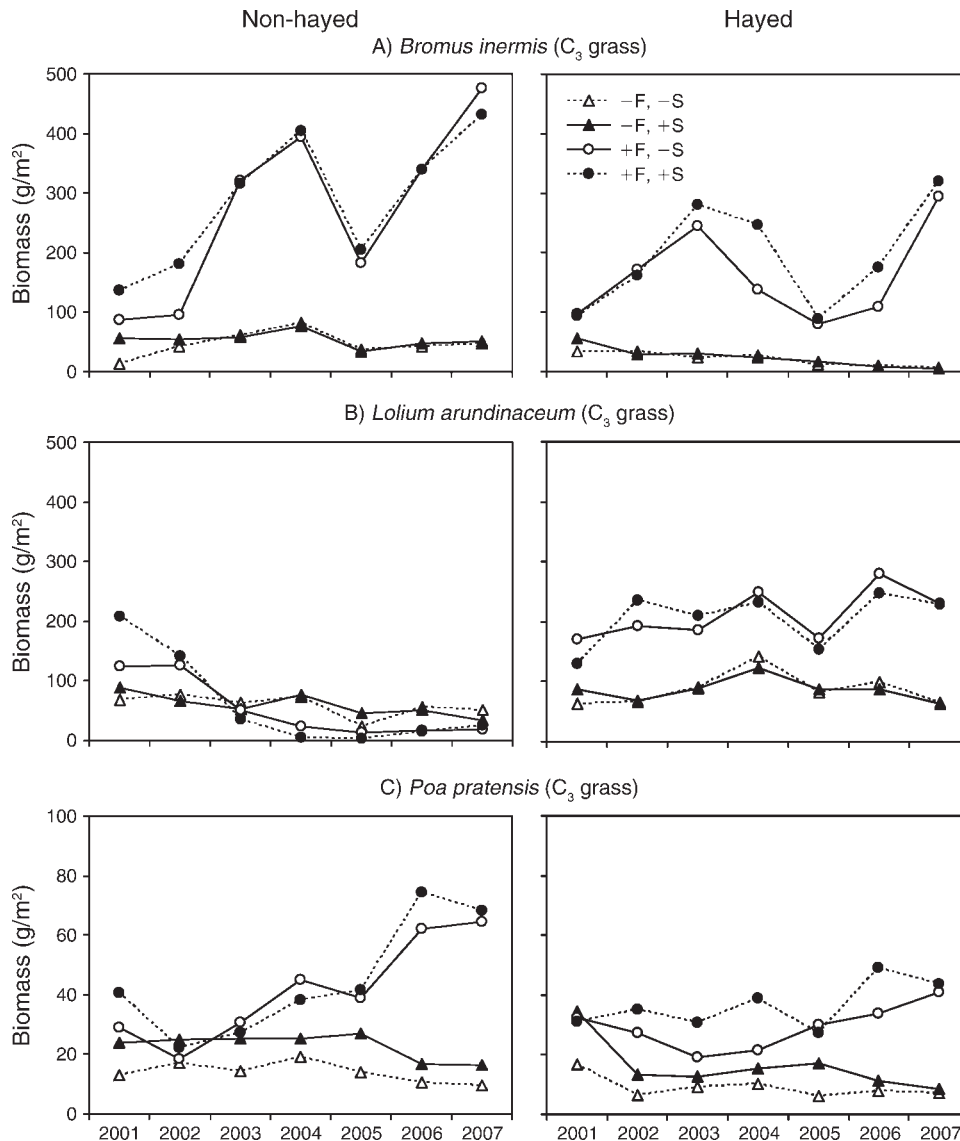
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FIG. 1. Treatment responses (mean biomass) of the three most abundant C_3 and C_4 grass species over the course of the study, 2001–2007. Treatments are: $-F$, non-fertilized; $+F$, fertilized; $-S$, non-sown; $+S$, sown ($n = 4$ replicate plots for each treatment combination).

response permutation procedure (MRPP; Zimmerman et al. 1985), operating on Euclidean distances, to evaluate significance of treatment effects on community composition apparent in the ordination. MRPP generates a chance-corrected within group agreement value (A) which evaluates the level of within treatment homogeneity of species composition (McCune and Medford 1999).

Temporal species turnover.—To examine treatment effects on plant community change occurring over the course of the study, we calculated three different measures of temporal community turnover for each of the 32 subplots: ST_O, ST_{RA}, and FGT. Each measure evaluates a different aspect of compositional turnover. ST_O, a measure of temporal turnover based on species

plot occupancy (species presence and absence), was calculated for each subplot using the qualitative Sorenson's index of dissimilarity. This index expresses turnover as the proportion of species shared between 2001 and 2007. ST_{RA} is a measure of temporal turnover between 2001 and 2007 based on changes in species relative abundances, and was calculated using the quantitative Sorenson's index of dissimilarity. FGT is a measure of temporal turnover in functional guild abundance between 2001 and 2007 calculated using the quantitative Sorenson's index of dissimilarity. Functional guilds used in the calculation of FGT were C_3 annual graminoids, C_3 perennial graminoids, C_4 annual graminoids, C_4 perennial graminoids, annual forbs, perennial leguminous forbs, perennial non-leguminous forbs, and
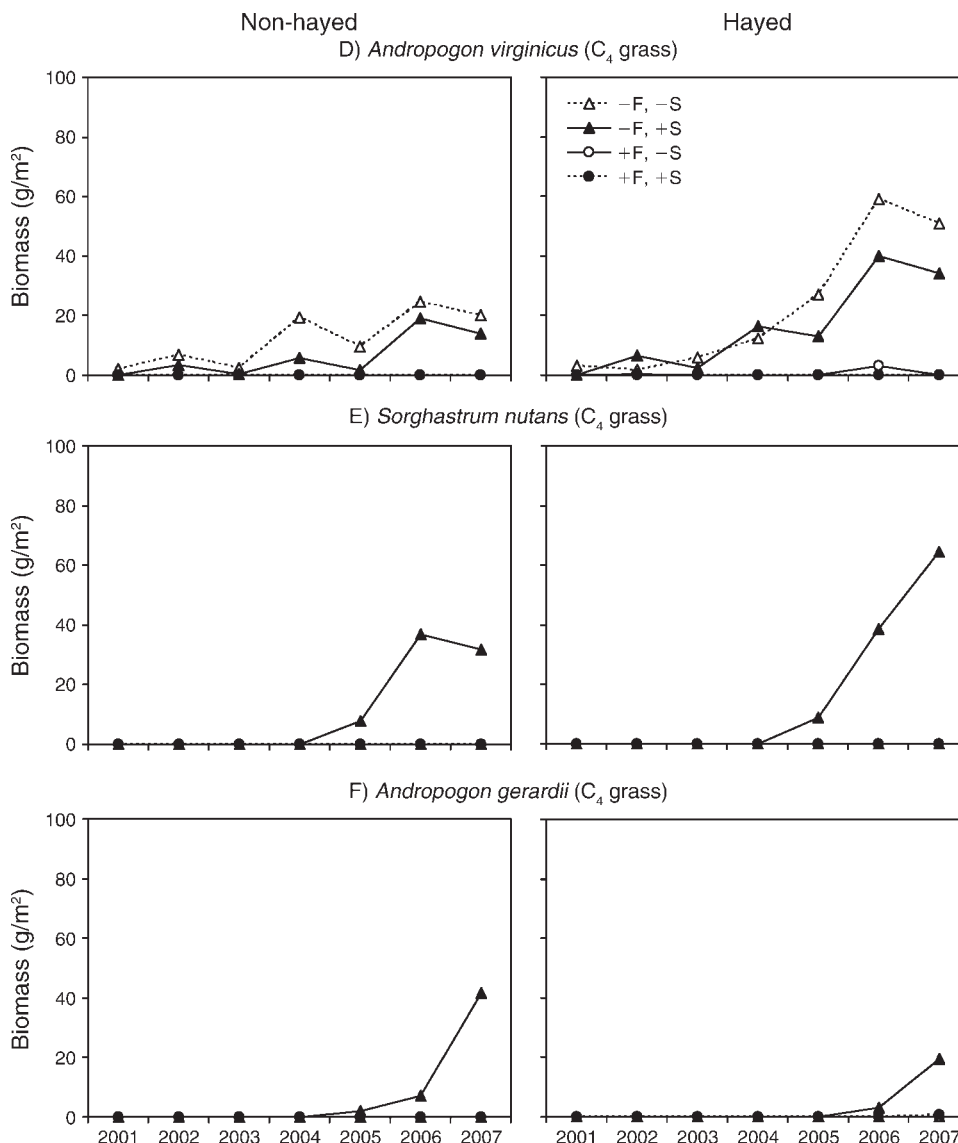
Non-hayed   Hayed

FIG. 1. Continued.

woody plants. All three measures of turnover were evaluated using within-subjects analysis of variance (ANOVA) with haying designated as a within-subjects factor and fertilization and sowing designated as between-subjects factors.

Data transformations and statistical programs.—The log_{10}-transformation was applied to biomass data and H' data to meet parametric assumptions of ANOVA. Statistical analyses were performed using SPSS for Windows (version 14.0; SPSS, Chicago Illinois, USA) and PC-ORD (version 2.0; McCune and Medford 1995).

RESULTS

Sown species establishment and plot occupancy

In 2007, five of the 41 sown species were recorded in a small percentage of non-sown plots, but only those that had not been fertilized (Table 1). Thirty-four sown species were recorded in at least one non-fertilized sown plot, with 20 of these species represented at plot frequencies of 50% or greater and 10 represented at 100%. In the fertilized sown plots, 12 sown species were recorded in at least one plot, but with only two species represented at plot frequencies of 50% or greater.

Species abundances

The three most abundant C_3 grasses at the start of the experiment, *B. inermis*, *L. arundinaceum*, and *P. pratensis*, responded differently to fertilization and haying (Fig. 1A–C). *B. inermis* biomass was strongly increased by fertilization, but to a lesser extent in hayed subplots. In the absence of fertilization, *B. inermis* biomass remained relatively stable over time in the
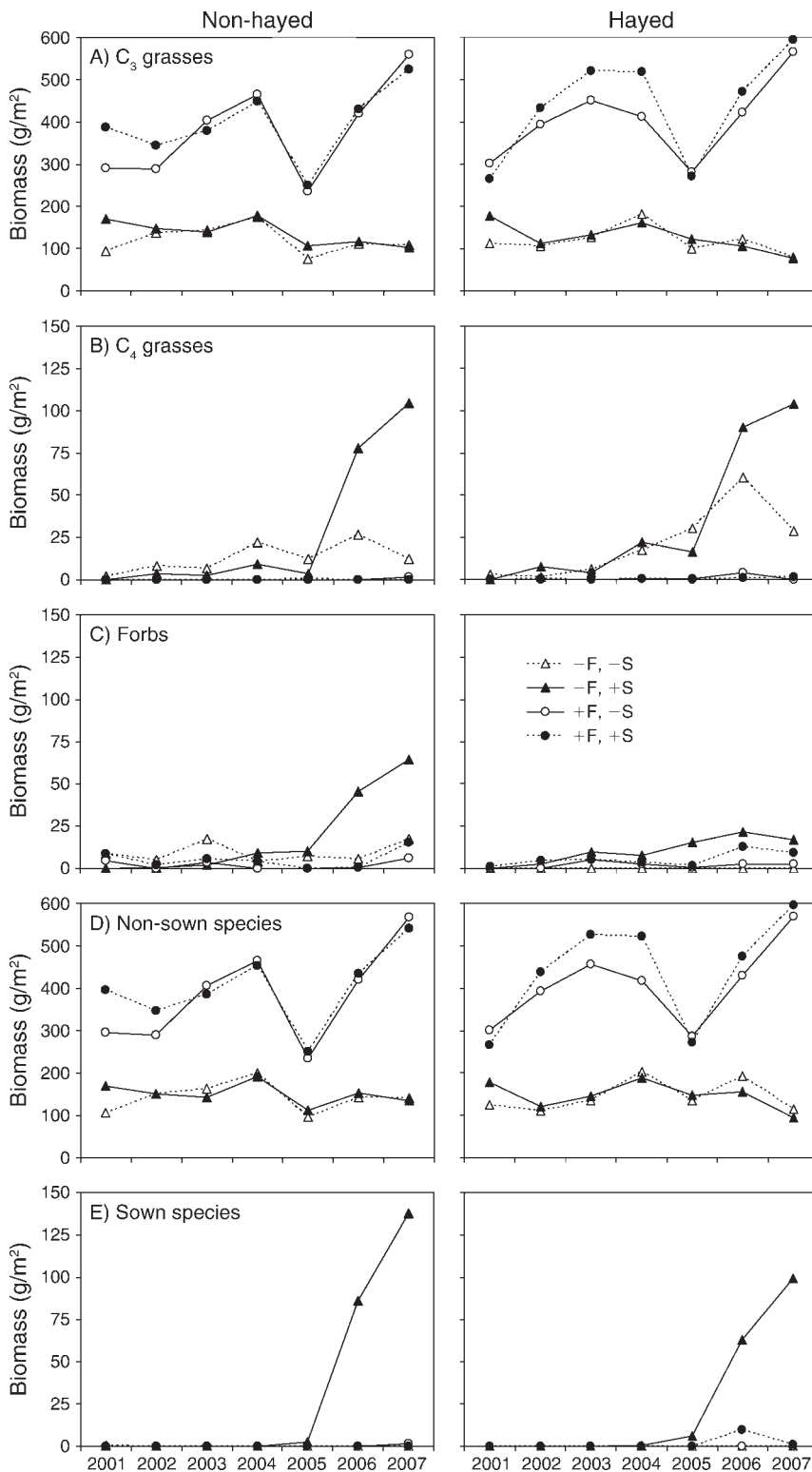
Fɪɢ. 2.   Treatment responses (mean biomass) of species aggregated as (A) C_3 grasses, (B) C_4 grasses, (C) forbs, (D) non-sown species, and (E) sown species. Treatments are: −F, non-fertilized; +F, fertilized; −S, non-sown; +S, sown ($n = 4$ replicate plots for each treatment combination).
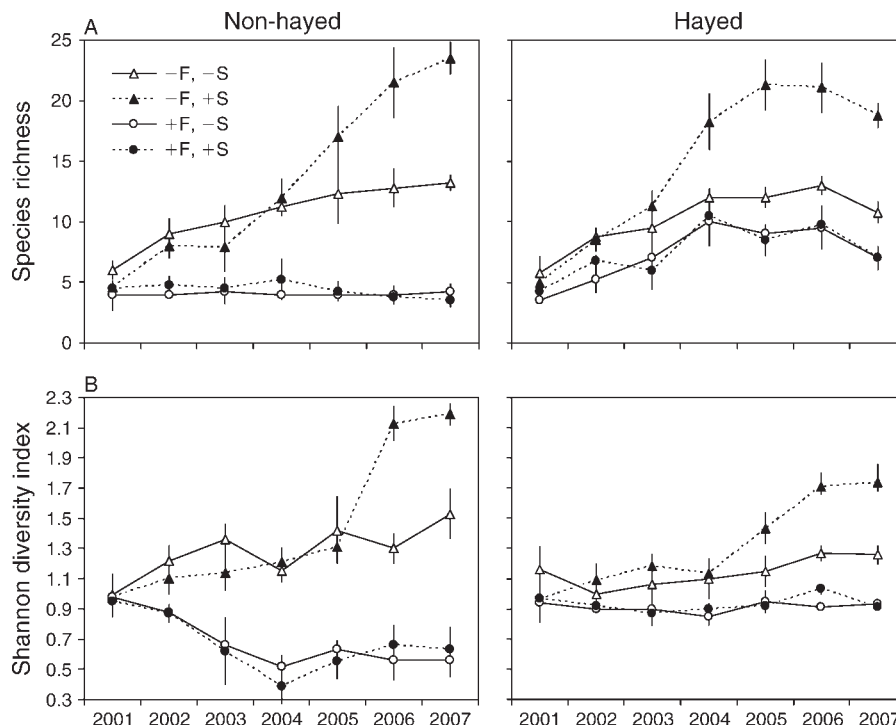
FIG. 3. Treatment responses (mean ± SE) of (A) species richness and (B) Shannon diversity index. Treatments are: −F, non-fertilized; +F, fertilized; −S, non-sown; +S, sown (n = 4 replicate plots for each treatment combination).

absence of haying, but declined steadily over time in the presence of haying. Fertilization increased *L. arundinaceum* biomass in hayed subplots and was relatively stable over time. However, in the absence of haying, *L. arundinaceum* declined over time in all other treatments with no apparent effect of fertilization. Like *B. inermis*, *P. pratensis* biomass increased with fertilization.

Andropogon virginicus, a native C_4 grass that began to naturally invade at the start of the study, and which was not sown in the experiment, increased over time in non-fertilized plots (Fig. 1D). This response was more pronounced in hayed subplots. *A. virginicus* remained virtually absent from fertilized plots throughout the study, regardless of haying treatment. The two most abundant sown C_4 grasses, *Sorghastrum nutans* and *Andropogon gerardii*, showed very similar dynamics as *A. virginicus*, but only in sown plots and only after they had been sown in 2003 (Fig. 1E, F).

In aggregate, C_3 grasses were greatly increased in biomass by fertilization, but showed no evidence of decline over time in non-fertilized plots (Fig. 2A). C_4 grasses were virtually absent from fertilized plots, but increased over time in non-fertilized plots (Fig. 2B). By 2006, C_4 grasses were most abundant in sown plots that had not been fertilized. Forb biomass was generally low throughout the study, but was increased by sowing in the non-fertilized subplots during the last two to three years (Fig. 2C). This response was most pronounced in the non-hayed subplots. Effects of fertilization on non-sown species in aggregate mirrored that of C_3 grasses

(Fig. 2D). Sown species biomass increased strongly after 2005 in only the sown plots that had not been fertilized (Fig. 2E).

Diversity

Species richness and Shannon diversity varied significantly among years and in response to fertilization, sowing and with a variety of interactions among factors, including the four-way interaction (Fig. 3, Table 2). Species richness and Shannon diversity index were both suppressed significantly by fertilization and these effects increased in magnitude over time, particularly in the non-hayed subplots and in plots that had been sown (year × fertilization × haying × sowing interaction; Fig. 3A, B). Haying increased richness and Shannon diversity in fertilized plots over most of the study, but either reduced or had no effect in non-fertilized plots, depending on the year (year × fertilization × haying interaction). Beginning midway through the study, sowing increased richness and diversity significantly in non-fertilized plots, but had no effect in fertilized plots (fertilization × sowing interaction).

Community composition

Fertilization, haying, and sowing all led to significant changes in species composition by the final year of the study (2007; Fig. 4). The singular effects of fertilization and haying on composition, as revealed by MRPP (Fertilization, $A = 0.34$, $P < 0.0001$; Haying, $A = 0.09$, $P < 0.01$), are evident in the NMDS ordination (Fig. 4A),

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TABLE 2. Within-subjects ANOVA evaluating variation in plant species richness, Shannon diversity index, and total plant biomass with respect to year (Yr), fertilization (Fert), haying (Hay), and sowing (Sow).

| Source	df	Species richness		Shannon diversity index		June standing crop biomass	
		MS	F	MS	F	MS	F
Within-subjects effects							
Yr	6	211.76	48.96***	0.42	17.26***	0.29	22.42***
Yr × Fert	6	80.23	18.55***	0.70	28.61***	0.05	3.94**
Yr × Sow	6	39.24	9.07***	0.24	9.61***	0.02	1.98
Yr × Fert × Sow	6	51.66	11.94***	0.13	5.48**	0.03	2.41*
Error(Yr)	72	4.325		0.02			
Hay	1	6.62	1.66	0.14	2.10	0.03	2.01
Hay × Fert	1	112.13	28.11***	2.15	31.13***	0.02	1.51
Hay × Sow	1	4.97	1.25	0.03	0.47	0.01	0.59
Hay × Fert × Sow	1	6.84	1.71	0.01	0.03	0.01	0.07
Error(Hay)	12	3.99		0.07		0.02	
Yr × Hay	6	193.36	37.25***	0.04	1.92	0.02	1.88
Yr × Hay × Fert	6	48.26	9.30***	0.15	6.72***	0.02	1.73
Yr × Hay × Sow	6	13.29	2.56*	0.06	2.80*	0.01	1.53
Yr × Hay × Fert × Sow	6	19.10	3.67**	0.05	2.30*	0.01	1.46
Error(Yr × Hay)	72	5.20		0.02		0.01	
Between-subjects effects							
Fert	1	1691.1	106.96***	13.05	100.72***	9.18	173.15***
Sow	1	156.76	9.91**	0.51	3.92*	0.27	5.03*
Fert × Sow	1	115.92	7.33*	0.52	4.02*	0.03	0.62
Error	12	15.81		0.13		0.05	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
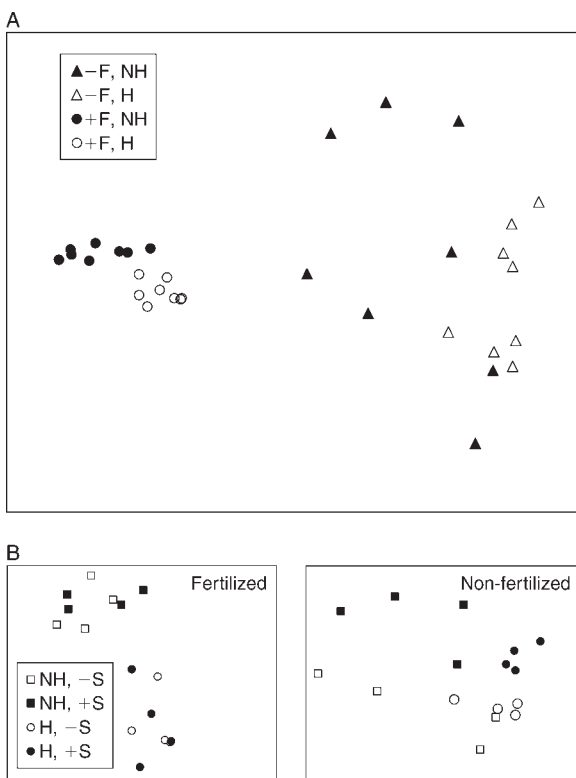
FIG. 4. Nonmetric multidimensional scaling (NMDS) ordination of the 32 experimental subplots in 2007, the final year of the study. (A) NMDS ordination coded by fertilization and haying treatments. (B) NMDS ordination partitioned by fertilization and coded by haying and sowing treatments. Treatments are: −F, non-fertilized; +F, fertilized; NH, non-hayed; H, hayed; −S, non-sown; +S, sown.

although the effects of haying were much more distinct among fertilized plots (Haying, $A = 0.45$, $P < 0.0001$) than the non-fertilized plots (Haying, $A = 0.08$, $P < 0.01$). Sowing significantly altered species composition, but only in the non-fertilized plots ($A = 0.15$, $P < 0.001$) as is apparent in the partitioned ordination of Fig. 4B.

Temporal species turnover

Species turnover (2000–2007) based on occupancy (ST_O) and on relative abundance (ST_{RA}) varied significantly with fertilization, sowing, with the interaction between fertilization and haying and with the interaction between fertilization and sowing (Fig. 5A, B). ST_{RA} also varied significantly with the main effect of haying. ST_O was greatly reduced by fertilization, slightly reduced by haying in non-fertilized plots, slightly increased by haying in fertilized plots, and increased by sowing only in the non-fertilized plots (Fig. 5A). ST_{RA} was greatly reduced by fertilization, slightly increased by haying in non-fertilized plots, decreased by haying in fertilized plots, and increased by sowing only in the non-fertilized plots (Fig. 5B). Functional guild turnover (FGT) varied with fertilization, sowing, and with the fertilization × sowing interaction (Fig. 5C). FGT was greatly reduced by fertilization, but was increased by sowing only in the non-fertilized plots.

Biomass

June standing crop varied significantly over time, with fertilization, with sowing, with the year × fertilization interaction, and with the year × fertilization × sowing interaction (Fig. 6A, Table 2). Fertilization increased June standing crop by a factor of 2.2 to 4.5, depending on year. Sowing increased June standing crop, but only
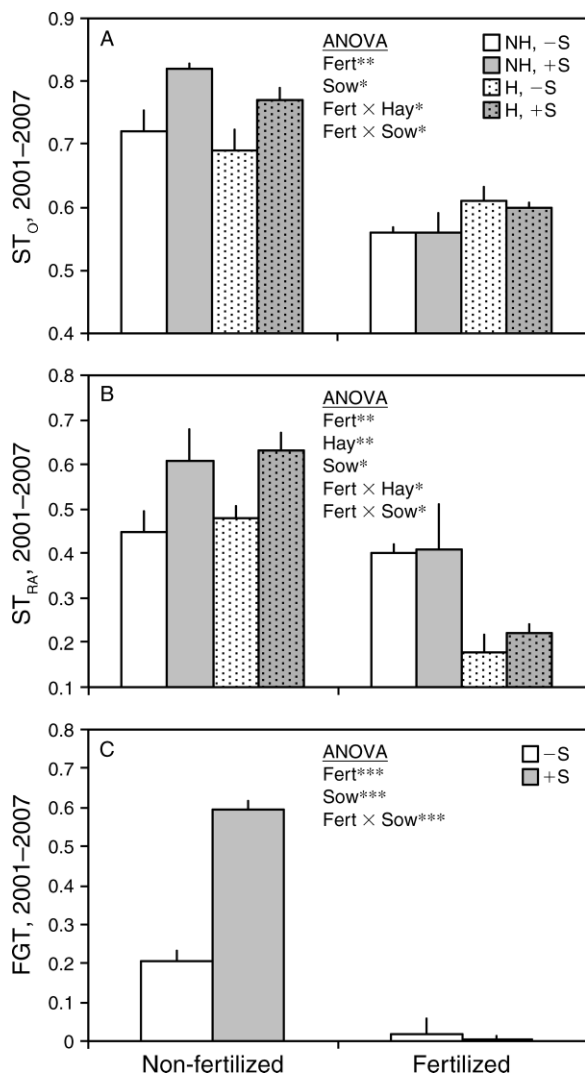
FIG. 5. Treatment differences in species turnover (ST, mean + SE) between 2001 and 2007 measured as turnover based on (A) species plot occupancy (ST_O), (B) species relative abundance (ST_{RA}), and (C) functional guild relative abundance (FGT). Significance levels are indicated by asterisks. Treatments are: NH, non-hayed; H, hayed; −S, non-sown; +S, sown ($n = 4$ replicate plots for each treatment combination).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

in non-fertilized plots during the last two years (fertilization × seed interaction; 2006, $F_{3,32} = 4.72$, $P < 0.05$; 2007, $F_{3,32} = 12.59$, $P < 0.01$). In the last year of the study, sowing had increased June standing crop in the non-fertilized plots by a factor of 2.1.

Peak-season standing crop measured in 2007 (June for fertilized plots, September for non-fertilized plots) varied significantly with fertilization, with sowing and with the fertilization × sowing interaction (Fig. 6B). Fertilization increased peak standing crop in the non-sown plots only. Sowing increased peak-season standing crop in the non-fertilized plots by a factor of 1.7, but had no effect in fertilized plots.

DISCUSSION

In this study, fertilization, haying, and sowing interacted strongly to influence species composition, diversity, and biomass, giving insights into the interplay of local and regional factors constraining community structure and ecosystem functioning. Here we discuss these findings in light of basic models of plant community organization and discuss implications for community and ecosystem restoration of former HILD hay fields to LIHD hay meadows.

Community structure and diversity

Our findings largely support the predictions of Huston (1999) and Foster et al. (2004) that low-fertility, low productivity communities are generally more open to colonization and relatively more limited by propagule availability than highly fertile and productive communities. Unlike the fertilized plots, non-fertilized plots were highly invasible, became increasingly diverse over time and exhibited high rates of compositional change measured as species turnover. The apparent instability and invasibility of non-fertilized plots is illustrated by the pattern of natural invasion by *Andropogon virginicus*, a non-sown species that began to colonize just as the
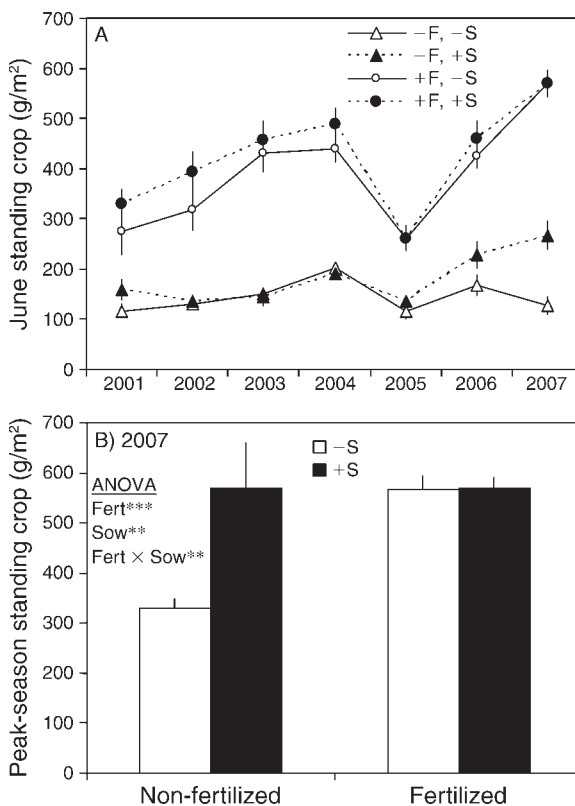

FIG. 6. Treatment responses (mean ± SE) of (A) June standing crop (for the years 2001–2007) and (B) peak-season standing crop for 2007 only. Treatments are: −F, non-fertilized; +F, fertilized; −S, non-sown; +S, sown ($n = 8$ replicate plots for each treatment combination of fertilization and sowing).

experiment started in 2000. *A. virginicus* is an opportunistic native C_4 grass that invades mid-successional old-fields throughout much of the midwest and eastern United States (Golley 1965). In 2000 and 2001, this species was virtually absent from all plots, but began to increase in the non-fertilized plots in 2002 and in much of the landscape that surrounded the experimental site (B. Foster, *personal observation*). *A. virginicus* was unable to invade fertilized plots, even those that had been hayed. The low abundance of *A. virginicus* at the field site at the start of the study is somewhat of a mystery, but may reflect the suppressive effects of prior hay management at the site and a recent history of fertilization. Our experimental results clearly show that fertilizer applications applied at rates typical for cool-season hay management effectively inhibit the colonization of this grassland by *A. virginicus* and by a variety of others species.

Results from the sowing treatment further illustrate the suppressive effect of fertilization and high production on community invasibility. In non-fertilized plots, sowing increased plant colonization, species composition, species and functional guild turnover and species diversity, indicating strong seed limitation of community structure and dynamics. In contrast, sowing had little influence on the fertilized communities, suggesting that the productive fertilized plots are resistant to invasion and thus limited more by micro-site availability and competitive exclusion than by seed availability. This finding is mirrored by the results of several studies of grassland diversity and restoration conducted in North America (Houseman and Gross 2006, Foster et al. 2007, Dickson and Foster 2008) and in Europe (Pärtel et al. 2000, Smith et al. 2000, 2003). For example, Smith et al. (2003) found that hay meadow restoration in a mesophytic grassland in the UK was most successful in the absence of fertilization and in the presence of haying disturbance. Across a wide gradient of Estonian grasslands, Pärtel et al. (2000) found that species diversity was relatively more limited by species pools in oligotrophic than productive systems.

The shifting limitations hypothesis (Foster et al. 2004), models by Huston (1979, 1999), and Grime (1979) and a variety of empirical studies (Whicker and Detling 1988, Collins et al. 1998, Wilson and Tilman 2002, Houseman and Gross 2006) indicate that moderate disturbances should to some extent counteract suppressive effects of high fertility and high productivity on invasibility and diversity. Our results largely support this prediction. Richness and Shannon diversity were increased by haying in fertilized plots, although not to levels of diversity found in non-fertilized plots. Species turnover in terms of species-plot occupancy was also increased by haying in fertilized plots, albeit by small magnitude, suggesting that haying created establishment opportunities in fertilized plots that would otherwise be unavailable. Interestingly, species turnover in terms of relative abundance was reduced by haying in fertilized

plots. This appears to reflect the ability of fertilization and haying, applied in combination, to maintain relatively stable abundances of the three most abundant C_3 hay grasses, *B. inermis*, *L. arundinaceum*, and *P. pratensis* (Fig. 1). In contrast, *L. arundinaceum* declined rapidly over time to very low abundances in fertilized subplots that were not hayed, suggesting that this species is not capable of coexisting with *B. inermis* under fertilized conditions unless plots are hayed.

Although haying did tend to counteract the negative effect of fertilization on natural colonization and diversity, it did not prevent fertilization from suppressing the establishment of sown species, contrary to our initial prediction. Under fertilized conditions, we expected haying to enhance establishment of sown species relative to non-hayed subplots. The rationale for this prediction was that haying disturbance would free resources, remove litter and create opportunities for establishment of available species that would otherwise be competitively excluded. It may be that haying in June is too mild of a disturbance and is ill timed to prevent competitive suppression of establishment by native prairie species under highly fertile conditions. Regrowth of the cool-season grasses prior to haying in spring was vigorous in fertilized plots, particularly those that had been hayed. These conditions are probably competitively unfavorable for the establishment of native C_4 grasses and other natives which begin their growth later in the season than the C_3 grasses.

To summarize our results for community dynamics, our findings suggest that in the absence of continued fertilization, former cool-season hay fields become unstable, open to invasion and will undergo succession towards dominance by C_4 grasses and increased native diversity. Rates of invasion, succession and accumulation of native diversity is strongly seed limited in these systems and thus occurs faster when seed limitations are overcome by restorative sowing.

Biomass yield

Using June standing crop biomass harvested from this experiment, our estimates of cool-season hay yields from the fertilized plots ranged from 2600 to 5500 kg/ha depending on year. This is within the range of yields for fertilized cool-season hay observed in eastern Kansas: 2242–7842 kg/ha (Lamond et al. 1992). June hay yields ranged from 2.2 to 4.5 times greater in fertilized plots than in non-sown, non-fertilized plots, illustrating the importance of annual fertilization to maintain high yields in cool-season hay fields.

Toward the end of the study, experimental sowing increased June hay yield, but only in non-fertilized plots where many of sown species were able to colonize, flourish and contribute to production. These findings suggest that, in the absence of fertilizer inputs needed to maintain C_3 grass dominance, biomass production is constrained by the availability of native seed sources. These results indicate the importance of diminished

species pools to both community and ecosystem development and with respect to restoration in human-impacted landscapes. The findings are also consistent with the hypothesis that plant diversity positively influences ecosystem processes (Tilman et al. 2001, Loreau et al. 2002). Although diversity and biomass were greatest in non-fertilized plots that were supplemented with native seed, the experimental design does not allow us to isolate a direct effect of increased plot diversity on yield from an effect of individual species or functional guild included in the seed mix. Our results do suggest that native diversity of the broader regional propagule pool is important in the regulation of local-scale ecosystem functioning and productivity by determining the availability of native species to colonize local sites (Grime 1998).

Analyses of yields in June allowed assessment of how experimental treatments affected production under cool-season management typical to eastern Kansas (June cutting). However, by the seventh year of the study it became clear that biomass harvested in June underestimated biomass production in non-fertilized plots, which by that time had become dominated by native C_4 grasses that attain peak biomass later in the season than C_3 grasses. This underestimation of yield in non-fertilized sown plots was confirmed in 2007 when we examined responses of peak-season biomass.

Our analysis showed that sowing increased peak biomass in non-fertilized plots up to a level indistinguishable from that of fertilized plots. In essence, addition of native species to non-fertilized plots compensated for the potential loss of productivity resulting from the cessation of fertilization. This comparison likely underestimates the long-term positive impact of native species restoration on overall ecosystem productivity at our site because (1) we did not account for effects on root biomass, which is typically much greater under native than nonnative grasses at our site (Foster et al. 2007); and (2) peak biomass in this study was measured fairly early in the restoration process: four years after sowing. As native species likely increase further in abundance over time we expect to see further increases in production in the restored plots. This expectation is supported by one of our other studies at the same field site where prairie sown plots achieved peak-season biomass ranging from 822 to 969 g/m^2 in 2005, five years after sowing (Foster et al. 2007). This level of peak biomass is considerably greater than that observed in the current study in restored plots in 2007 (mean of 578 g/m^2) or in the fertilized plots in any year of this study (June biomass minimum of 302 g/m^2 in 2001 to a maximum of 568 g/m^2 in 2007).

It is important to note that peak biomass measured in our study, which was harvested in early September 2007 for the non-fertilized plots, may overestimate yields of warm-season hay as intended for use as animal forage. This is because forage hay is typically cut in mid July–early August when hay quality (protein content) is still relatively high, but before peak production has been reached. So although our measure of peak biomass provides an estimate of season maximum yield, which may be suitable for use as biofuel, it likely overestimates to some extent yields expected under traditional warm-season hay management. Still, our findings suggest that restorative sowing of abandoned HILD hay fields may compensate for declines in production resulting from the cessation of fertilization, and may at least partially compensate for losses in forage hay yield.

CONCLUSIONS

Our results support the shifting limitations hypothesis of community organization and highlight the importance of species pools and seed limitations in constraining successional turnover, community structure, and ecosystem productivity under conditions of low fertility. Our findings also indicate that several of the biological and functional aspects of LIHD hay meadows can be restored from abandoned HILD hay fields by ceasing fertilization and by reintroducing native species through sowing. Our findings suggest that declines in primary production and hay yield that result from cessation of fertilization may be at least partially compensated for by restoration with native species. Although it is difficult to generalize the findings of field experiments, our study does suggest that as fertilizer prices increase and as additional commodity options for LIHD hay become available (such as for biofuel), conversion of HILD hay fields to LIHD hay meadows may become a viable alternative for some land owners, particularly those that factor into their decision making the ecosystem services and the various aesthetic and conservation benefits provided by restoration.

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