Effects of Frequent Mowing on Survival and Persistence of Forbs Seeded into a Species-Poor Grassland

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Abstract

Many early attempts at tallgrass prairie reconstruction failed to achieve the high species diversity of remnant prairies, and instead consist primarily of C_4 grasses. We hypothesized that frequent mowing of established prairie grasses could create sufficient gaps in the aboveground and belowground environment to allow for the establishment of native forbs from seed. We studied forb seedling establishment in a 25-year-old prairie planting in northern Iowa that was dominated by native warm-season grasses. In winter 1999, 23 species of native forbs were broadcast into the recently burned sod at a rate of 350 viable seeds/m^2. Treatment plots were mowed weekly for either one or two growing seasons, and control plots were unmowed. Mowed plots had greater light availability than controls, especially when warm-season grasses began to flower. Overwinter seedling mortality was 3% in mowed treatments compared to 29% in the controls. Forbs in mowed plots had significantly greater root and shoot mass than those in control plots in the first and second growing seasons but were not significantly more abundant. By the fourth growing season, however, forbs were twice as abundant in the mowed treatments. No lasting negative impacts of frequent mowing on the grass population were observed. Mowing a second year influenced species composition but did not change total seedling establishment. Experimental evidence is consistent with the idea that mowing reduced competition for light from large established grasses, allowing forb seedlings the opportunity to reach sufficient size to establish, survive, and flower in the second and subsequent years.

Key words: forb enhancement, gap, mowing, prairie reconstruction, recruitment, seedling establishment, species-poor grassland, species richness, tallgrass prairie.

Introduction

Although ecological restoration often means starting over on a newly cleared site, it is sometimes better to retain the established vegetation and enhance its species diversity or composition. Species diversity may be lower than desired due to partial failure of the first restoration planting, or species losses due to exotic species invasion or fire suppression. Enhancing the diversity of established plant communities poses special challenges because they can be highly resistant to colonization by new individuals.

The same resistance occurs in natural communities. It is widely recognized that most tree seedlings will fail to survive unless they occur in a forest canopy gap (e.g., Pickett & White 1985). Gaps are equally important in the colonization of grasslands. Disturbance-generated gaps in grasslands have been investigated in many environments including British chalk grasslands (Davies et al. 1996), fens (Isselstein et al. 2002), the Flint Hills prairie of Kansas (Rogers & Hartnett 2001), northern Great Plains mixed grass prairie (Wilson & Pärtel 2003), Kangaroograss (*Themeda australis*) grassland in Southeast Australia (Hitchmough et al. 1996; Morgan 1997), California coastal grasslands (Maron & Jeffries 2001) and old fields (Goldberg & Werner 1983). Seed germination may occur in many locations, especially if not impeded by litter, but survival of seedlings is generally restricted to larger canopy gaps due to the elevated availability of physical space, light, moisture, and nutrients). Smaller gaps are quickly reoccupied by vegetative reproduction and spread of the surrounding plants unless the gaps are constantly maintained (Bullock et al. 1995; Hitchmough et al. 1996; Rogers & Hartnett 2001). The effect of gaps on seedling survival and size is most evident in environments with high fertility and moisture and less important in communities with low productivity (Goldberg & Werner 1983; Davies et al. 1996; Foster et al. 2004).

On mesic tallgrass prairies most similar to the present study site, Rapp and Rabinowitz (1985) found that disturbances characteristic of small animal excavation were initially occupied by waves of seedlings and shoots but that none established. This result was largely a function of the small (5.8-cm diameter) gaps that became heavily shaded during the growing season. In contrast, Collins et al. (1998) studying Kansas Flint Hills prairie found that large plots grazed or mowed throughout a growing season had

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greater species richness than controls, due to a combination of new seedling establishment and the release of suppressed individuals.

Over the past 30 years, native tallgrass prairie grasses have been seeded on conservation reserve lands and public road rights-of-way (Smith 1998). Many of the native plantings in the 1960s through the early 1980s had few or no native forbs in the seed mix because forb seeds were not commercially available. A survey sent to public land managers in Iowa indicates that thousands of hectares of species-poor C_4, perennial grasslands exist with essentially no native forb component (Williams, unpublished data). The lack of plant diversity in these restored grasslands compared to remnant prairies is a cause for concern because in locations like Iowa, prairie remnants are isolated fragments and may occupy as little as 0.1% of their original extent (Smith 1998). In such cases, spread and establishment of prairie forbs will probably not occur naturally due to the almost complete lack of propagules and extremely long distances from remnant seed sources.

Species-poor grasslands may negatively impact the diversity of other species in these areas. Ries et al. (2001) found more butterfly species and more individuals in grasslands containing native forbs than those without. Sutter and Brigham (1998) found that the invasion of crested wheatgrass, while reducing overall botanical and structural diversity, had little effect on the grassland bird community; however, Wilson and Belcher (1989) discovered significant differences in the native bird community in transects dominated by Eurasian vegetation. Pepper (1999) found that species diversity of arthropods was positively correlated with grassland size. Beyond this, species-poor grasslands have little conservation value as corridors or steppingstones between fragments of remnant prairie. Habitat fragmentation has been identified as a factor that contributes to the loss of native plant species in remnants (Leach & Givnish 1996). Enhancing species-poor grasslands with forbs could reduce distances between native plant and invertebrate populations.

There is substantial evidence that diverse grasslands can inhibit weed invasion. Wilson and Pärtel (2003) and Bakker and Wilson (2004) found that removing the invasive grass *Agropyron cristatum* by herbicide and mowing facilitated invasion by the native grass *Bouteloua gracilis*, and that plots seeded with mixtures of native grasses resisted *A. cristatum* invasion while allowing the invasion of other native species. Blumenthal et al. (2003) tested the effect of restoration on weed populations in a Minnesota old field by experimentally restoring prairie species using intensive, high-disturbance, and seed-only methods compared to unmanipulated controls. Seven years after the experimental treatments, intensively restored plots had significantly lower weed biomass and cover than the control treatment.

However, at the scale of the county, Stohlgren et al. (2003) found a positive correlation between native and non-native species richness. Smith and Knapp (1999) found on Kansas tallgrass prairie, native species richness and exotic species richness were positively correlated across sites subjected to a range of fire and grazing treatments and within a single disturbance regime. The outcome of this debate is of particular interest to public agencies such as state and county departments of transportation, who spend millions of dollars each year to eradicate non-native, weedy plants from roadsides planted to just two or three species of grass.

For these reasons, the study presented here tests methods for enriching existing grasslands with native forbs by creating gaps in the stand of mature grasses using mowing, a method available to most grassland managers. There are no documented efforts to enhance species-poor grasslands using gap formation in the most endangered prairie communties, the mesic tallgrass prairie. Kurtz (1994) and other experienced prairie restorationists have observed that frequent mowing during the first growing season after a new prairie seeding increases establishment. We applied Kurtz's frequent mowing technique to introduce forbs by seed into an established tallgrass prairie planting without destroying the existing vegetation. We hypothesized that frequent mowing in the first year after broadcast seeding would increase light intensity at ground level and enhance forb growth relative to controls. We further hypothesized that a second season of mowing might aid in the establishment of late germinating species or those that are very slow growing. Finally, we predicted that the effects of mowing treatments on seedling establishment would persist beyond the first 2 years of the experiment.

A secondary question, the effect of planting time, was investigated within one mowing treatment. We hypothesized that there would be differences in emergence and establishment depending on time of planting.

Methods

Study Site

The reconstructed tallgrass prairie study site (lat 42°30′30″N, long 92°27′00″W) is part of the University of Northern Iowa Biological Preserves in Cedar Falls, Iowa. It is a small alluvial bench of about 6 ha along a creek with a mixture of loamy soil over sand and gravel (Fouts & Wisner 1982). Prior to 1973, the site was a hayfield dominated by Smooth brome (*Bromus inermis*), Quackgrass (*Agropyron repens*), and Red clover (*Trifolium pratense*). In spring 1973, the hayfield was plowed, disked, and seeded with 24.7 kg/ha of cultivated varieties of native, warm-season (C_4) perennial grasses. The seed mix consisted of Big bluestem (*Andropogon gerardii*), Little bluestem (*Schizachyrium scoparium*), Switchgrass (*Panicum virgatum*), Side-oats grama (*Bouteloua curtipendula*), and Indiangrass (*Sorghastrum nutans*). The site was divided into subunits and each unit burned every 2–3 years since seeding. Presently, the site is similar to other grass-dominated plantings of the 1970s. Cool-season (C_3) Kentucky bluegrass (*Poa pratensis*), and Smooth brome (*B. inermis*) are responsible for most of the leaf area in spring and fall, whereas warm-season grasses dominate in mid-summer. Although there is a small (approximately 400 m^2) patch of native forbs established by transplant in one corner of the reconstruction, only one species, Rattlesnake master (*Eryngium yuccifolium*), has spread beyond this area.

Experimental Design

The experiment was a randomized block design with two blocks and two treatments: mowing (control, one season, two seasons) and time of seeding (winter and spring seeding, nested within one mowing treatment). Blocks (60 × 60 m) consisted of 12, 15 × 20–m plots; no sampling was done within 1 m of plot perimeters. Block centers were 100 m apart and mapped as the same soil type. There were no obvious initial differences in plant cover or species composition between blocks.

In each block, three replicate plots were randomly assigned to an unmowed control or one of two experimental mowing treatments. The mow-1 treatment (mowed for one growing season, 1999) was randomly assigned to six plots per block; and the mow-2 treatment (mowed for two growing seasons, 1999 and 2000) was randomly assigned to three plots per block. In 1999, there were three control and nine mowed plots per block; in 2000 there were three control and six mow-1 and three mow-2 plots per block.

A seeding time treatment (winter vs. spring) was nested within the mow-1 treatment. Control, mow-1, and mow-2 treatments were first burned on 23 October 1998 and seeded 3 November 1998 (Control and mow-1) or 24 February 1999 (mow-2). These three treatments were all considered a "winter seeding," because they all occurred while the soil was frozen and vegetation was dormant. The spring seeding, mow-1s ($N = 3$ plots per block), was burned 19 April 1999 and seeded on the following day. Thus, within the mow-1 treatment, we were able to compare the effects of winter and spring seeding.

We considered but rejected the option of a no-seed control. The study area had been planted 26 years prior and had apparently not experienced significant new species colonizations since that time. Portions of the prairie adjacent to the experiment remained species-poor throughout the study.

Seed Preparation and Experimental Treatments

Seed of Iowa origin was purchased from a Northeast Iowa prairie nursery (Table 1). Seeding rates and species composition reflected common practices for this region and soil type. (When seeds were purchased, the project was conceived as an unreplicated, practical demonstration for county roadside managers, but was subsequently redesigned as a formal replicated experiment.) Seed was broadcast by hand after mixing with sand. During the first growing season, we mowed weekly from 1 May to 1 September using

Table 1. Forb species composition and seeding rate used for the experiment, ordered by viable seeds sown.

Species	*Family*	*Mean Seed Mass (g)*	*Pure Live Seed (%)*	*Viable Seeds (No. sown/m²)*
Aster novae-angliae	Asteraceae	0.00008	60.00	134.7
Rudbeckia hirta	Asteraceae	0.00026	81.94	56.7
Solidago rigida	Asteraceae	0.00036	82.25	28.1
Ratibida pinnata	Asteraceae	0.00095	89.10	22.2
Dalea purpurea	Fabaceae	0.00143	81.93	13.5
Monarda fistulosa	Labiatae	0.00035	80.79	13.1
Coreopsis palmata	Asteraceae	0.00084	60.00	12.8
Anemone cylindrica	Ranunculaceae	0.00108	87.92	10.0
Liatris pycnostachya	Asteraceae	0.00120	83.52	8.6
R. subtomentosa	Asteraceae	0.00067	60.00	7.6
Lespedeza capitata	Fabaceae	0.00255	87.16	6.1
Euphorbia corollata	Euphorbiaceae	0.00246	81.91	4.1
L. aspera	Asteraceae	0.00180	59.70	4.1
Echinacea pallida	Asteraceae	0.00368	82.54	4.0
Heliopsis helianthoides	Asteraceae	0.00493	83.34	4.0
Tradescantia ohiensis	Commelinaceae	0.00382	56.10	3.7
Desmanthus illinoensis	Fabaceae	0.00452	90.67	3.6
Amorpha canescens	Fabaceae	0.00278	60.33	2.7
A. canadensis	Ranunculaceae	0.00319	69.45	2.7
Asclepias tuberosa	Asclepidaceae	0.00504	69.52	2.5
Zizia aurea	Apiaceae	0.00341	69.11	2.5
Desmodium canadense	Fabaceae	0.00430	85.67	2.4
Silphium laciniatum	Asteraceae	0.03234	63.79	0.5

Mean seed weight was calculated from a subsample of 10 seeds from each species. An independent seed lab (Hulsey Seed Laboratory Inc., Decatur, GA, U.S.A.) tested for pure live seed.

a turf-grass riding mower. The initial mowing height was 5 cm and increased gradually to 10 cm by 1 July and to the mower's maximum of 13.5 cm in August to accommodate forb growth. We mowed every 2 weeks during the second growing season (2000) from 1 May to 1 September using a three-point rotary mower attached to a 22 hp John Deer tractor with turf tires. The initial mowing height of 13.5 cm was gradually increased to 27 cm by early July.

Light and Plant Community Measures

A LI-COR 190 quantum sensor (LI-COR Biosciences, Lincoln, NE, U.S.A.) was used to measure photosynthetic photon flux density (μmols m^{-2} s^{-1}). A sampling location was randomly selected in each plot and used for all measurements. Light readings were taken at ground level, every 2–3 weeks during the growing season during 1999, at approximately solar noon on clear days. We recorded five readings at each location and averaged them for analysis. To assess the effects of mowing treatments on native grass abundance, basal area (cm^2/m^2) of the warm-season grasses was measured in all plots. Basal area was estimated in each 0.25-m^2 subplot in September 1999 and 2000.

Seedling Emergence and Mortality

For measurement of seedling emergence, seven randomly placed 0.25 m^2 permanent quadrats were established in each plot. The quadrats, constructed of polyvinyl chloride potable tubing and formed into a circle, were affixed to the ground with heavy gage wire. We identified and counted seedlings in all quadrats at bimonthly intervals from June to September 1999 and monthly intervals from June to September 2000 to maximize detection of forb seedling emergence and mortality. Seedlings grown in the greenhouse aided in field identifications; typically this was possible soon after the first true leaf had formed, within 2 weeks of emergence. A seedling was counted only if it could be positively identified to species.

Forb Size, Maturity, and Long-Term Persistence

To determine if mowing affected forb growth, we destructively sampled 20 plants from each of four perennial species *Ratibida pinnata*, *Solidago rigida*, *Echinacea pallida*, and *Monarda fistulosa* in each treatment in September 1999 and 2000 (160 plants/yr). Belt transects 1-m wide were randomly located in one randomly selected mow-1 plots and one control plot in each block. We then collected the first 10 individuals encountered. The use of variable plot size addressed our concern that the very smallest plants, often hidden by larger plants, might inadvertently be undersampled in plots of fixed size.

We used a bulb planter to extract 5-cm diameter × 15-cm plugs, which were washed over a 1-cm mesh screen. Parts of other plants were separated from the target individual to expose intact roots and shoots. Maximum root and shoot lengths were measured with a tape measure, then all plant parts were oven dried (60°C) to constant mass and biomass determined. In 1999, very few plant roots extended beyond the 15-cm length of the soil plug. In 2000, several plants in the mowed treatments exceeded 15 cm, so root length data are not present for this year, and root biomass represents root mass in the upper 15 cm of soil. With the exception of this group, however, measures of root length and biomass of these young seedlings were thought to accurately represent root size.

To assess plant maturity, we counted flowering plants in six control and six randomly selected mow-1 plots in late June, early August, and mid-September 2000. Data were pooled across sampling dates to determine the maximum number of flowering plants by species regardless of bloom time. Because of the abundance of *Rudbeckia hirta*, a 20 × 1–m belt transect was established randomly to estimate flowering in this species.

We determined long-term persistence of established forbs by census on 20–25 May 2003, using 20 × 1–m belt transects established randomly within each replicate plot. These plots had not been disturbed since the original experiments. Forbs over 3 cm in height and possessing at least one true leaf were counted. Only forbs this large were considered because they represent individuals that have a reasonable expectation of reaching maturity and/or becoming established. Common forbs (*R. pinnata*, *R. hirta*, *S. rigida*, and *Aster novae-angliae*) were identified to species; other species were counted but not identified.

Data Analyses

All data except forb size and maturity were analyzed using analysis of variance (ANOVA) or repeated measures ANOVA to evaluate changes over time. To test for the assumptions of ANOVA, skewness (g1), kurtosis (g2), and homoscedasticity (Bartlett's test) were first calculated for all data sets. A Student's t test ($\alpha = 0.05$, with infinite degrees of freedom [*df*]) was conducted to determine if the data had significant skew or kurtosis and residuals were examined (Wilkinson 1989). Data sets determined to be nonnormal were either log-transformed or square root transformed to achieve normality and homogeneity of variances. Means were back-transformed to report the data.

The full ANOVA model initially applied to all analyses included five sources of variation: block, mowing treatment, seeding time nested within mow-1, block × mowing, and block × seeding time. It was determined that seeding time had no significant main effects or interactions in any analysis, so winter- and spring-seeded treatments were combined for subsequent analysis (Allen & Cady 1982). The simplified model had three sources of variation: block, mowing, and block × mowing. Means and tests of significance reported here were based on the three-source model unless otherwise noted. The General Linear Models program in Systat (Wilkinson 1989) was used for all ANOVAs.

The model and error *df* differed between years. In the first year, the mow-2 treatment did not yet exist (all mowed plots were treated identically), resulting in two levels of mowing, 3 *df* in the model, and 20 *df* in the error term. In 2000, we ceased mowing the mow-1 plots and continued mowing the mow-2 plots, so there were three treatment levels (control, mow-1, and mow-2), 5 *df* in the model, and 18 *df* in the error term. For year 2000 data, individual treatment means were compared with Tukey's protected test for pairwise comparisons.

Seedling emergence and mortality were evaluated for the sum of all species due to the generally small number of seedlings per species. Seedlings were analyzed by repeated measures ANOVA in three ways: trends in live seedling numbers within each growing season (eight sample dates in 1999 and four dates in 2000), assessment of growing season mortality by comparing maximum emergence with end of season seedling numbers, and assessment of overwinter mortality by comparing seedling numbers in mid-September 1999 with 1 June 2000.

The maximum number of emerging seedlings per square meter in each plot was calculated by summing the maximum number of seedlings of each species in each quadrat over the season and dividing by the square meters sampled. Because different species' numbers peaked at different times in each quadrat within a plot, this provided the most sensitive data set for maximum emergence. Biweekly sampling minimized the under-reporting of seedlings that emerged and died between counts, and repeated measures ANOVA allowed us to detect small treatment differences, which would otherwise be overwhelmed by plot to plot variation.

Data for forb size in 1999 and 2000 were pooled across the four species to assess general effects of the mowing treatments and reduce the number of individual means comparisons; data were log-transformed prior to analysis to achieve normality and homogeneity of variances and back-transformed for presentation. The experimental unit for plant size was interpreted as the individual plant, so treatment differences were analyzed using a Students *t* test, with a Bonferroni correction to limit type I error.

The comparison of forb maturity was done informally because most of the species observed flowering in the mow-1 plots in 2000 were never found flowering in any of the control plots and thus had zero variance in that treatment.

Results

Light Intensity and Plant Community Response to Mowing

Mowing significantly ($p < 0.001$) increased light intensity in all plots (Fig. 1). This became most pronounced in the beginning on 9 July, when development of the C_4, perennial grass canopy accelerated due to reproductive culm elongation. Light levels after 9 July never exceeded 200 μmol s^{-1} m^{-2} in the control plots, compared to 750–1100 μmol s^{-1} m^{-2} in mowed plots. Monthly rainfall during summer 1999 ranged from 5 to 20 cm above the 30-year average (NOAA 1999).

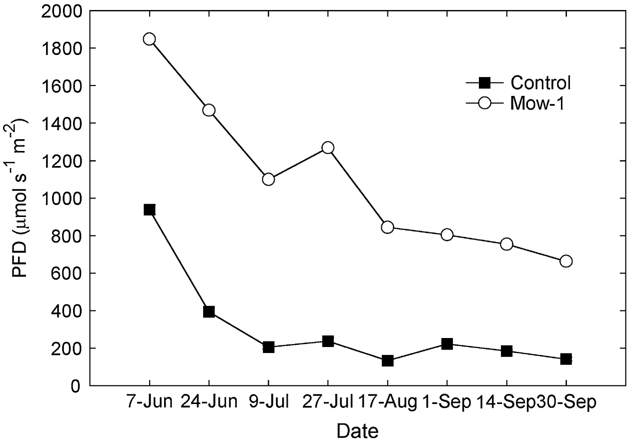

Figure 1. Mean photosynthetic photon flux density and SE (all bars are within treatment symbols) measured at ground surface near solar noon in mowed and control plots during the 1999 growing season (LI-COR Biosciences). Mowing height and forb growth in mowed plots helped to reduce incident light over the growing season. The canopy of warm-season grasses that developed in early July reduced light in control plots. Reported means were back-transformed from log-transformed data.

There were no significant effects of mowing on the basal area of C_4 grasses in either year. We observed that mowed plants had many, small shoots compared to the few, large shoots in control plots. Repeated measures ANOVA comparing treatments between 1999 and 2000 showed a significant ($p = 0.013$) reduction in basal area among mowed treatments, from 15.3 (±1.35) to 11.2 (±0.43) cm^2/m^2 in mow-2, compared to controls, from 12.8 (±1.25) to 12.0 (±1.25) cm^2/m^2. However, there were significant ($p = 0.046$) block × mowing effects, so the negative effect of mowing on basal area of the preexisting warm-season grasses was not firmly demonstrated.

Seedling Emergence and Mortality

A total of 2,170 seedlings were observed across quadrats, plots, treatments, and species in 1999. There was no evidence of a treatment effect of seeding time or mowing in the average number of live seedlings over summer 1999 (Fig. 2). However, repeated measures ANOVA revealed a significant difference in the seasonal pattern between mowed and control treatments. In mowed plots, the number of living seedlings increased steadily throughout the summer, whereas in control plots, they peaked in late June and then decreased as the summer progressed ($p = 0.020$; Fig. 2).

Repeated measures ANOVA comparing maximum seedling emergence with end of season seedling number in 1999 showed a significant ($p = 0.033$) interaction between time and mowing treatment (Table 2). Seedlings in control plots were reduced 42%, whereas seedlings in mowed plots were reduced 29%. Mowing had an even

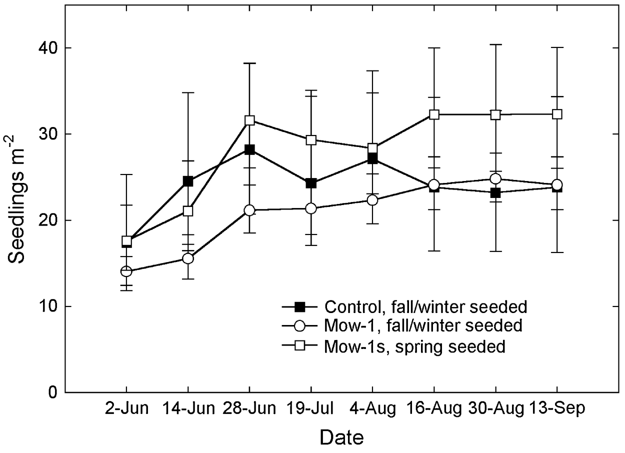

Figure 2. Mean forb seedling numbers and SEs by mowing treatments in 1999. Control and mow-1 plots were seeded in fall/winter 1998 and mow-1s plots were seeded in spring 1999. Mowing was done weekly in 1999. Repeated measures ANOVA test of seedling means by mowing treatment over all sample times in 1999 showed a significant ($p = 0.02$) increase of seedlings in mowed plots over time. Reported means were back-transformed from log-transformed data.

stronger effect on overwinter seedling mortality, with controls decreasing 29%, whereas those in mowed plots decreased only 3% ($p = 0.002$; Table 2). Mowed plots tended to show a lower rate of seedling mortality (16–24%) compared to controls (28%) in 2000, but this was not significant ($p = 0.072$; Table 2).

Species composition of the seedlings for the most part reflected what was sown (Fig. 3). All but one of the 23 seeded species (*Tradescantia ohiensis*) was found in the 24 plots. The top six planted species represented 77% of the seeds and 86% of the first years' seedlings. There were two notable exceptions: *Rudbeckia hirta* was over-represented among the seedlings, and *Aster novae-angliae* was greatly under-represented. In the second year, a total of 370 new seedlings from 10 species were found in the permanent plots, 66% of these from *R. hirta*. Other species experiencing second-year germination included *Ratibida pinnata*, *Echinacea pallida*, *Helianthus helianthoides*, *Anemone cylindrica*, *Asclepias tuberosa*, *Euphorbia corollata*, *Zizia aurea*, *Silphium laciniatum*, and *Amorpha canescens.*

Forb Size, Maturity, and Persistence

Forbs in mowed plots, while necessarily shorter than the height of the mower's cutter bar, were significantly taller and more deeply rooted than forbs in the control plots and had significantly greater biomass (Table 3). This trend continued into the second year. Two-year-old plants, which were destructively sampled in September 2000, were 223% taller in the mowed area than the control. They also had 16.5 times more shoot mass and 13 times more root mass than control plants. By 2000, eight species were flowering in mowed plots versus two species in control plots (Fig. 4; Table 4). The only species with more than one flowering individual in the control plots was *R. hirta*, and it was 32 times more abundant in the mowed plots.

At the beginning of the fifth growing season (in May 2003), there were more than twice as many forbs greater than 3 cm high in mow-1 and mow-2 plots (6.1 and 5.8 plants/m^2, respectively) than in controls (2.6 plants/m^2; $F = 22.4$, $p < 0.001$, $df = 2, 18$). Among the common forbs, only *Solidago rigida* responded significantly to the length of mowing, comprising 10% of the common forbs in control plots, 18% in mow-1, and 27% in mow-2 plots ($F = 6.37$, $p = 0.008$, $df = 2, 18$).

Discussion

Any process that diminishes the size of dominant individuals while leaving small plants virtually untouched should

Table 2. Change in number of seedlings over time analyzed by repeated measures ANOVA in summer 1999, over the winter 1999–2000, and in summer 2000.

	Mean Seedlings/m^2		*Repeated ANOVA (p values, Measures within-subjects effects)*			
Treatment	*Maximum/Beginning*	*End*	*Time*	*Block*	*Mow*	*Block × Mow*
Maximum and end of summer 1999			<0.001	0.094	0.033	0.506
Control	40.4 (31.2–52.4)	23.5 (16.3–33.9)				
Mow-1	37.1 (33.8–40.7)	26.5 (23.6–29.6)				
End of summer and beginning of spring (overwinter mortality 1999–2000)			<0.001	0.140	0.002	0.185
Control	23.5 (16.3–33.9)	16.6 (10.8–25.6)				
Mow-1	26.5 (23.6–29.6)	25.7 (22.7–29.1)				
Maximum and end of summer, 2000			<0.001	0.233	0.072	0.161
Control	21.6 (15.1–31.0)	15.5 (10.1–23.7)				
Mow-1	33.0 (28.2–38.6)	27.8 (23.4–33.1)				
Mow-2	30.0 (26.6–33.7)	22.6 (20.4–25.1)				

Calculation of maximum seedling numbers is given in the text. Within-subjects effects test for interactions between treatments and the change in numbers from one time to the next. Means are back-transformed from their natural logs for presentation and SEs are presented as a range, ±1 SE

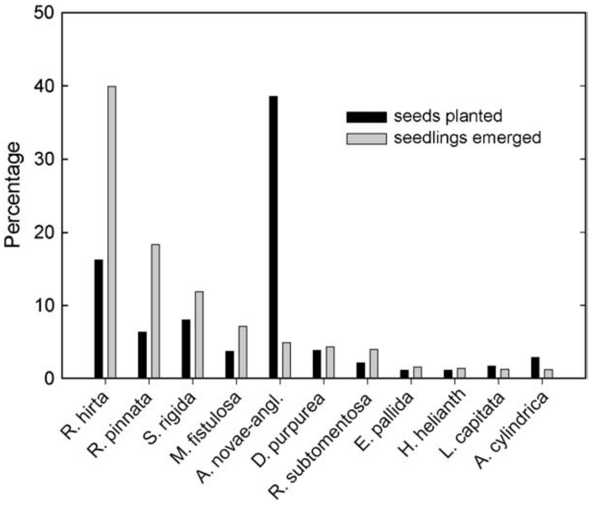

Figure 3. Comparison of species composition of seeds planted (as percentage of seeds planted) and species emerging (as percentage of total) in 1999 for 11 of the most abundant species. These species accounted for more than 95% of all seedlings found in all samples.

promote the establishment of new individuals in a previously closed community. We hypothesized that mowing grassland vegetation and overseeding with forbs would create favorable conditions for establishment of forb seedlings. Once emerged, seedlings in mowed plots grew larger and matured more quickly than those in control plots.

Mowing increased light availability and likely influenced the emergence and survival of forb seedlings in mowed plots. Once the canopy of warm-season grasses closed in mid-July, net seedling numbers in control plots began to decline, whereas in mowed plots, they continued to increase gradually. In agricultural systems, the closure of the crop canopy is a pivotal event in weed management because weed seedlings die or are permanently suppressed (Liebman et al. 2001). Peltzer and Köchy (2001) and Peltzer and Wilson (2001) showed that removing neighboring vegetation increased percent light penetration as well as soil nutrients, and that the presence of neighbors significantly reduced the size of experimental seedling transplants by 33–89% in both prairie and forest environments.

Table 3. Mean (SE) of shoot and root lengths and biomass of forbs in September 1999 and 2000 ($N = 80$ in each year).

	Control	*Mow-1*	*p Value*
Plant size (cm)			
Shoots 1999	5.4 (0.49)	8.9 (0.33)	<0.01
Shoots 2000	13.7 (0.96)	30.5 (1.12)	<0.01
Root 1999	6.3 (0.45)	8.2 (0.44)	<0.01
Biomass (g)			
Shoots 1999	0.019 (0.010)	0.134 (0.018)	<0.01
Shoots 2000	0.080 (0.016)	1.320 (0.239)	<0.01
Root 1999	0.008 (0.010)	0.034 (0.013)	<0.01
Roots 2000	0.020 (0.097)	0.260 (0.048)	<0.01

Roots lengths for 2000 are not reported because they often exceeded the length of the harvesting tool (>15 cm). Root biomass in 2000 is for the first 15 cm. Means were log-transformed and analyzed by Student's *t* test with a Bonferroni correction to limit type I error.

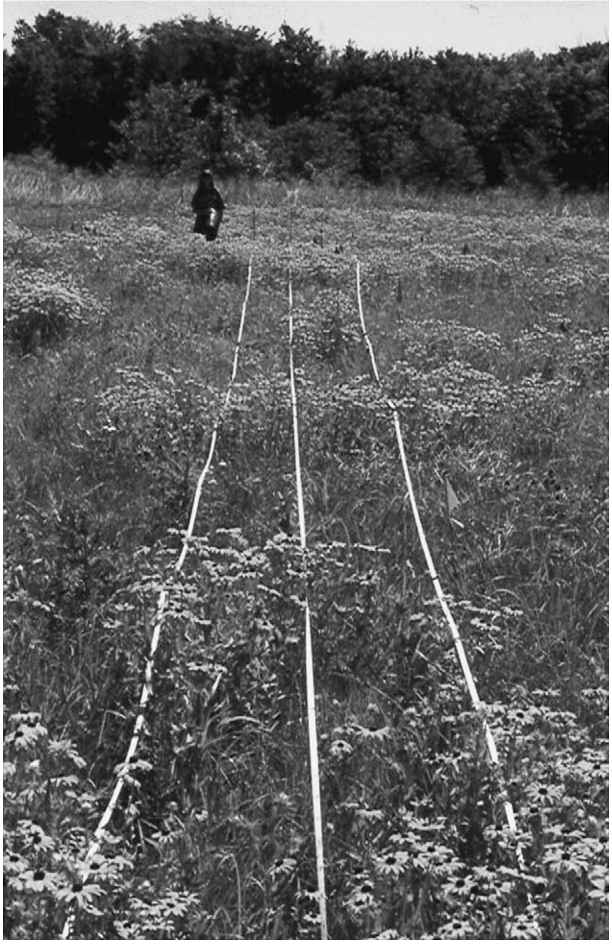

Figure 4. Mowed research plots in June 2000 illustrating extensive forb establishment.

Despite evidence of reduced mortality in mowed plots, particularly over the winter of the first year, seeded forbs were still equally abundant (15–28 plants/m^2) in mowed and control treatments at the close of the second growing season. However, by the beginning of year 5, the introduced forbs greater than 3.0 cm tall were only half as abundant in the control treatment (2.6 vs. 5.8 to 6.1 plants/m^2, $p < 0.001$). We attribute this to the superior size of forbs in mowed plots, and their ability to compete with established grasses once mowing ceased. Although no formal measures were taken of percent cover, we observed that the seeded forbs gradually increased in size from year to year, becoming more visually dominant and eventually flowering and producing seed. Boundaries between

Table 4. Total number of forbs flowering in six mow-1 and six control plots counted in year 2 of 2000. Results were pooled from three counts to accommodate differences in flowering times among the species.

Species	*Mow-1 Plot*	*Control Plot*
**Rudbeckia hirta*	6,660	210
Aster novae-angliae	164	0
Heliopsis helianthoides	114	0
Solidago rigida	43	0
Ratibida pinnata	7	0
Desmodium canadense	3	0
Dalea purpurea	1	1
Lespedeza capitata	2	0

*Estimate based on 20 m^2 sample per plot.

mowed and control plots were still visible in 2005, due to the striking contrast in forb abundance.

It is likely that belowground changes created by mowing also contributed to forb establishment. Biswell and Weaver (1933) demonstrated that frequent aboveground leaf clipping of Big bluestem (*Andropogon gerardii*) and Switchgrass (*Panicum virgatum*) greatly reduced root biomass and rhizome growth within one growing season, creating gaps in the root zone. Johnson and Matchett (2001) using root ingrowth techniques found that heavily grazed patches in Flint Hills tallgrass prairie produced 30% fewer roots than fenced controls. Two lines of evidence suggest an important role for reduction of competing grass roots in the repeatedly mowed plots. First, basal area of warm-season grass stems at ground level decreased by 27.7% in mowed plots, the second year, and this may reflect a reduction in rooting volume to some extent. Second, forb roots in mowed plots in 2000 had 13 times more root mass than plants from control plots.

We hypothesized that mowing in the second year would extend the period of new seedling emergence and establishment, particularly for species that do not germinate immediately, but this effect was limited. It is possible that few viable forb seeds remained in the soil in the second growing season, due to natural sources of mortality, and the excellent conditions for seed germination that prevailed in 1999. This result could vary with the weather and species of seed used in an experiment and should be tested again under different conditions. By the fourth growing season, it was clear that extended mowing had increased establishment of *Solidago rigida* compared to both control and mow-1 plots. Other species (*Ratibida pinnata*, *Aster novae-angliae*, and *Rudbeckia hirta*) did not respond or did not occur in sufficient numbers to compare treatments.

The initial selection of species and seeding rates reflected a typical seed mixture for northeastern Iowa prairie reconstructions, with emphasis on the inexpensive, early-flowering biennial *R. hirta* and other early successional species in the Asteraceae. Consequently, the results reflect primarily the corporate response of about 11 species comprising 95% of the seedlings germinating. The results of this experiment are influenced not only by the year of establishment but also the particular mixture of species and seed abundances used and may be expected to differ with other seed mixtures.

We have observed that attempts at tallgrass prairie reconstruction often result in low levels of species richness compared to the initially diverse seed mixture (personal author observations) and are usually much less diverse than the native prairie remnants they emulate (Polley et al. 2005). Practitioners may gain important insights from basic research into the question of what determines species richness at the local scale (Zobel et al. 2000; Foster et al. 2004; Zobel & Kalamees 2005). These studies have examined the relative importance of seeds versus the availability of areas where competition from other plants is reduced (gaps or microsites). In general, areas of high primary productivity and low disturbance tend to be microsite limited, whereas areas of low primary productivity or high disturbance tend to be seed limited. Disturbance becomes more important for new seedling establishment where standing biomass or primary productivity is high.

The experimental site used in the present study is typical of many reconstructions in the tallgrass prairie biome both in terms of primary productivity and seed availability. It is relatively high in productivity due to an average of 842 mm rainfall (NOAA 1999) and deep (84 cm to the B horizon), loamy soils formed under perennial grass vegetation (Fouts and Wisner 1982). Annual net primary productivity has not been measured at this site, but vegetative cover is virtually 100% each year, and the prairie grasses *A. gerardii* and *Sorghastrum nutans* reach 2 m height.

Although the regional species pool (Pärtel 2002) at this site is potentially rich with over 360 native plant species recorded in the nearest remnant tallgrass prairie 14 km away, it is functionally poor due to the conversion of 99.9% of tallgrass prairie to cropland (Smith 1998) and consequently long dispersal distances. Species diversity is likely limited first by the low propagule availability of the regional species pool. Then, in the rare event of seed dispersal to the site, seedlings must compete with well-established, highly productive existing vegetation.

Our data support this general picture. The observation that initial seedling establishment was equal in mowed and control plots supports the importance of propagule availability, but greater overwinter seedling mortality, smaller plant size, and lower long-term persistence of forbs in control plots confirms the importance of competitive exclusion in this highly productive setting. Particularly in the mesic, nutrient-rich soils of the North American tallgrass prairie, recruitment of new individuals to an established plant community will require a disturbance or opening that is large and persistent enough to provide new seedlings a "head start" against competing fully grown plants. In the past, this could have been accomplished by large herbivores, but they are absent from most protected prairie remnants today. It is currently unknown whether species richness in tallgrass prairie remnants can be maintained indefinitely without occasional disturbance events leading to new recruitment.

Conclusions

"Successional restoration" was described by Packard (1994) as enhancing diversity by sowing native species without destroying the established vegetation. Christiansen (1994) found spring burning to be a successful management technique to increase native prairie grasses and forbs sown into an established stand of cool-season grasses. There are many instances, however, in which burning is not an optimal treatment and mowing is already employed. Along midwestern county and state public right-of-ways, burning is often prohibited for safety concerns. Our research suggests that the addition of seed and a single year of managed mowing could transform right-of-way grassland strips and other species-poor grasslands into more diverse plant communities. It would be useful to determine whether similar seedling establishment results can be achieved with less frequent mowing than was used in the present study. Landowners with grazing animals may be able to modify this approach using intensively managed grazing instead of mowing (Jackson 1999).

This research confirms the experience of practitioners (Kurtz 1994) and offers a strategy for building upon the work of the early prairie reconstruction era of the 1960s and 1970s in which forb seed was largely unavailable. Unlike new seedings, successional restoration does not require intensive management beyond the first growing season, providing direct economic benefit to the landowner and is relatively inexpensive to implement. Transformation of these previously sown, species-poor grasslands into more complex plant communities will take us closer to restoring some native plant diversity to the former tallgrass prairie landscape.

Implications for Practice

- Species-poor prairie plantings composed of warm-season grasses may be diversified with new forb species through burning, overseeding, and weekly mowing.
- Seeds were hand broadcast at 350 seeds/m^2 (23 native species) in winter or spring after burning.
- Mowing was weekly beginning 15 May and mowing height was raised gradually from 5 to 14 cm to reduce damage to forbs.
- Season of planting (winter vs. spring) did not affect seedling establishment.
- One season of mowing was no worse than two seasons.
- Forbs grew larger in mowed plots and flowered after 2 years. By the fifth year, forb density was 6 plants/m^2 in mowed plots compared to 2.6 plants/m^2 in control plots.

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