Do fire and seed additions alter strong seed timing and priority effects on prairie establishment?

Leanne M. Martin
Department of Ecology, Evolution and Organismal Biology,
Iowa State University,
Ames, IA 50011

Dr. Brian J. Wilsey
Department of Ecology, Evolution and Organismal Biology,
Iowa State University,
Ames, IA 50011

Introduction and Objectives

Many prairie restoration projects in the United States and Iowa have been planted, and many more are being established (Mlot 1990, Smith 1998). However, many projects are somewhat hampered by a lack of knowledge on how to restore the high diversity found in prairies, while at the same time preventing the establishment of a large weedy component. Furthermore, the diversity of existing plantings is often much lower than the diversity of native prairie remnants and has high numbers of exotic species (Mlot 1990, Packard and Mutel 1997, Martin et al. 2005, Polley et al. 2005). Therefore, methods are needed to increase diversity and abundance of native species while minimizing exotic species invasions in both 1) newly planted restorations and 2) established restorations.

One method that has been proposed to simultaneously establish native seedlings and prevent weed invasion in new restorations is to plant a cover crop prior to seeding the native prairie species (Shirley 1994). This idea is based on the assumption that the cover plant will act as a nurse plant to the prairie seedlings, and will have a positive effect on seedling recruitment by increasing weed suppression and by lowering the harmful effects of high evaporation and light availabilities. Furthermore, little is known about how timing of planting during the growing season affects establishment of prairie versus weeds and resulting diversity of restorations.

Previously, we established an experiment in Story and Monona counties in 2005 to determine the effects of different native cover crop species and timing of seeding on the establishment of new prairie restorations. We found that after six years adding the mix in early spring led to diverse, native communities, but adding the mix in the late summer or the following year after cover crops established led to low diversity communities dominated by exotics, and these differences were evident in the field (Fig. 1) (Martin and Wilsey, submitted). Cover crops did not increase recruitment of the prairie mixture or increase diversity, and they did not lower proportion of exotics in the restoration plots as predicted (Martin and Wilsey, submitted). The spring seeded plots also had higher fuel mass, fire temperatures, and peak aboveground net primary productivity, suggesting these treatments can affect important processes in prairies

(Martin and Wilsey, submitted). These results were consistent between both sites. Overall, therefore, results from the first part of this experiment suggest that seeding new prairie restorations in the early spring with no cover crop will produce the highest prairie species establishment.

Figure 1. A diverse, native-dominated treatment (left photo) which resulted when the prairie mixture was seeded in the spring with the cover crops; and a low-diversity, exotic-dominated treatment (right photo), which resulted when the prairie mixture was seeded in the summer, or when it was seeded a year after the cover crops were seeded.

Our original experiment tested differences in establishment of new prairie, and here we test one strategy to improve established, low diversity and exotic-dominated prairie restorations. Here, we report results on species composition after a second seed addition was added to ash after a spring fire in half of the Monona County plots. Williams et al. (2007) found that overseeding grass dominated plantings with forb seed mixes could increase forb abundance when plots were burned before seeding, and mowing after seeding enhanced forb abundance. However, seed was added in winter in their study, and here we added seed in spring, the time when the most native species established in our original experiment. The objectives of this study were to:

1) Determine if the timing of seeding continues to affect prairie species diversity and native species abundance.
2) Determine if native cover crops have any long term effects on prairie species diversity and native species abundance.
3) Determine if seed additions added to ash after spring fires can increase prairie establishment and species diversity and alter biomass in divergent, established prairie communities.

These objectives were addressed by sampling old plots (objectives 1 and 2), and with seed additions to a subset of Story County plots in 2010, the sixth year of the study, and in Monona County plots in 2011, the seventh year of the study. Results from Story County plots were reported last year, and we found that seed additions did not increase diversity or abundance from the mixture, and they did not lower exotic proportions after one year. Here, we report results from the second seed addition to Monona County plots in spring 2011. We burned all existing cover crop and seed timing experimental plots in Monona County from the original experiment in spring, 2011, and added a seed addition treatment to half of the plots immediately after burning to determine if adding seed after fire could significantly increase prairie establishment in low-diversity prairie restorations. Dividing the existing treatments into seeded and non-seeded plots allowed us to continue monitoring the effects of the original cover crop and seed timing plots, which are valuable for informing new restorations, as well as testing a new method to improve existing restorations.

Methods

Study sites and Cover Crops

Experimental plots were set up on slopes near roadsides at the Iowa State University farms near Ames (Horticulture Farm, a mesic site) and at the Western Research and Demonstration Farms (a dry site) near Castana in Monona County in 2005.

Seed mixes were added to plots that contain one of 6 cover crop treatments: 1. No cover crop (control), 2. Canada wildrye (*Elymus canadensis*), 3. Partridge pea (*Chamaecrista fasciculata*), 4. Black-eyed susan (*Rudbeckia hirta*), 5. Side-oats gramma (*Bouteloua curtipendula*), 6. All four species combined.

These 6 treatments have been applied to experimental plots at each of the two sites (Story and Monona Counties). These two sites were selected because 1) they represent a mesic and a dry site and broader generalizations can be made as a result, and 2) they represent sites that are conveniently located for the PI, with the Ames site close to ISU and the Monona County site close to other projects. All plots were placed on slopes so that they are more relevant to roadside plantings.

Original Experimental Design

During 2005, we established a cover crop experiment on the effects of seeding dates at each of the two sites using a split-plot experimental design. Plots of 5 x 5 m were marked out at each of the two study areas. Each plot was then split up into four 2 x 2 m subplots with 1 m corridors between them. Each subplot received one of four treatments: 1) spring 2005 planting of cover crop with prairie seed mix, 2) spring 2005 planting of cover crop with prairie seed mix added one year later (spring 2006), 3) summer 2005 planting of cover crop with prairie seed mix, or 4) summer 2005 planting of cover crop with prairie seed mix added the following spring (spring 2006). Spring seeding was conducted in April 2005 by broadcasting the seed mix from Table 1 at the same rate of 10 lbs. per acre in tilled fields formerly dominated by brome.

Summer seeding was conducted in August 2005 on bare ground using the same broadcasting method. The cover crops included Canada wildrye, Side-oats gramma, Black-eyed susan, partridge pea, and all four cover crop species combined (mixed cover crops). The cover crops were compared to control plots that received the prairie mix only. The mixed treatment uses a mixture of all four cover crops, but has the same overall seed mass. For example, the mixed treatment contains 2.5 lbs per acre of each of the four species, or 10 lbs. per acre total, which is the same as the monoculture plots. This tested the idea that having all of the early emerging species included as a cover crop was better than having only one, perhaps as a result of weed suppression and because of the different microhabitats created by multiple species. There are five replicate plots of each of the main plot treatments (6 treatments) at each of the two sites (Horticulture farm in Story County and Western Research Farm in Monona County), for 30 x 2 = 60 main plots total, and 60 x 4 = 240 subplots total. Biomass of prairie and weed species was estimated with point intercept sampling, which involved counting all plant contacts with a metal pin dropped through the canopy in the middle of each plot during July of each year (Jonasson 1998).

Fire and Seed Additions: New Treatment Experimental Design

In spring 2011, we added a new treatment to the existing experiment in Monona County to determine if the strong differences exhibited by seed timing, cover crops and priority effects (adding prairie mixtures with the cover crop after they established) can be altered to increase prairie establishment, thereby converging the original treatments and increasing diversity. To do this, we burned all plots in Monona County in late April 2011, and over-seeded the original prairie seed mixture (less red root, *Ceonothus herbaceous*, and pasque flower, *Anemone patens* due to seed unavailability and because they have never germinated in the plots, and excluding the cover crops seeds) to half of the main plots at each site immediately after the burn (Table 1).

Since there are five replicates of six main treatments (cover crops) at each site, three main plots of each treatment were randomly selected at the Western Research Farm in Monona County. This resulted in 18 main plots (five of each cover crop) with the fire/seed addition treatment and 12 main plots with the fire treatment only at the Monona County site in 2011. Seeds were obtained from Custom Seed Company. Abundance of prairie and weed species was sampled in July 2011 using our point-intercept method. We have found that our point intercept method is highly correlated with biomass.

Results

After seven years of establishment of the restoration plots in Monona County, timing of the original seeding continued to have the strongest influence on the prairie communities, while changing the identity of cover crop was not significantly different. Diversity and abundance from the mix were 53% and 8 times higher, respectively, and proportion of exotic species was 45% lower when the original mix was added in the spring with the cover crop compared to when prairie mixture seeds were added in the summer or a year after cover crops (history treatments, diversity $F_{3,51}$ = 24.9, P < 0.01; mixture $F_{3,51}$ = 37.5, P < 0.01; proportion exotic $F_{3,51}$ = 31.3, P < 0.01) (Fig. 2). None of the variables differed among cover crop treatments (cover crops, diversity $F_{5,17}$ = 1.24, P =0.34; mixture $F_{5,17}$ = 0.41, P = 0.83; proportion exotic $F_{5,17}$ = 1.14, P = 0.38) (Fig. 3).

Adding a second 30-species prairie seed addition to half of the plots seven years after the original restoration plots were established did not significantly lower the proportion of exotic species but it increased diversity by 17% and increased the abundance from the 30-species prairie mixture by 16% overall (second seed addition, proportion exotic $F_{1,17}$ = 0.47, P = 0.50, diversity $F_{1,17}$ = 5.8, P = 0.03; mixture $F_{1,17}$ = 5.9, P = 0.03) (Figs. 2 and 3). Interestingly, however, diversity increased significantly only in the subplots that were already the most diverse (i.e., seeded in spring with the cover crop) (treatment x second seed interaction, $F_{3,51}$ = 3.09, P = 0.04), which means that low and high diversity plots did not converge to a similar diversity with seed additions as expected. Rather, they appeared to diverge even more, with diverse plots becoming more diverse. No other interactions with the original treatments and the second seed addition were significant (treatment x second seed interaction, mixture $F_{3,51}$ = 1.6, P = 0.20; proportion exotic $F_{3,51}$ = 0.55, P = 0.65; cover x second seed interaction, mixture $F_{5,17}$ = 1.4, P = 0.27, proportion exotic $F_{5,17}$ = 1.1, P = 0.39, diversity $F_{5,17}$ = 1.2, P = 0.35). Overall, even though there were slight increases in diversity and recruitment of species in the prairie mix, results from the first year of the second seed addition indicate that the original treatments did not converge with seed additions.

Species that increased slightly in abundance from the second round of seed additions were in most cases not different from the species that were already found in the unseeded plots (Table 2). Sixteen species out of the thirty species in the prairie mix increased to some degree in seeded plots, which means nearly half of the species in the seed mix are still absent in all of the plots. Out of the sixteen species that increased, three forbs and three grasses that were completely absent in treatments without a second seed addition were found in seeded treatments. (species in bold in Table 2). All other species were found in their respective treatments prior to the second seed addition. *H. helianthoides* was the only species that increased in abundance in all treatments, but that species was also present in all of the treatments prior to the second seed addition.

Table 1. Seed mix of prairie species that were added in the initial experiment after the cover crop was established, and again five years later to half the main plots at the Story County site after a spring fire, less *A. patens* and *C. herbaceous* due to seed unavailability and no germination.

Species	Family
Warm season grasses	
1. Little bluestem, *Schizachyrium scoparium*	Poaceae
2. Big bluestem, *Andropogon gerardii*	Poaceae
3. Indian grass, *Sorghastrum nutans*	Poaceae
4. Switch grass, *Panicum virgatum*	Poaceae
5. Tall dropseed, *Sporobolus asper*	Poaceae
Cool season grasses	
6. June Grass, *Koeleria macrantha*	Poaceae
7. Porcupine Grass, *Stipa spartea*	Poaceae
Forbs	
8. Wild Bergamot, *Monarda fistulosa*	Lamiaceae
9. Bottle Gentian, *Gentiana andrewsii*	Gentianaceae
10. Butterfly Milkweed, *Asclepias tuberosa*	Asclepiadaceae
11. Dotted[1] or Rough[2] Blazing Star, *Liatris aspera and punctata*	Asteraceae
12. Ground Plum, *Astragalus crassicarpus*	Fabaceae
13. Hoary Vervain, *Verbena stricta*	Verbenaceae
14. Lead Plant, *Amorpha canescens*	Fabaceae
15. Pale purple[1] and Narrow Leaved[2] Coneflower, *Echinacea angustifolia* and *pallida*	Asteraceae
16. New Jersey Tea, *Ceanothus americanus*	Rhamnaceae
17. Ox-eye, *Heliopsis helianthoides*	Asteraceae
18. Prairie Phlox, *Phlox pilosa*	Polemoniaceae
19. Prairie Larkspur, *Delphinium virescens*	Ranunculaceae
20. Prairie Rose, *Rosa arkansana*	Rosaceae
21. Purple Prairie Clover, *Dalea purpurea*	Fabaceae
22. Red Root, *Ceanothus herbaceus*	Rhamnaceae
23. Round_headed Bush Clover, *Lespedeza capitata*	Fabaceae
24. Smooth Aster, *Aster laevis*	Asteraceae
25. Stiff Goldenrod, *Solidago rigida*	Asteraceae
26. White Prairie Clover, *Dalea candidum*	Fabaceae
27. Yellow Coneflower, *Ratibida pinnata*	Asteraceae
28. Primrose, *Oenothera biennis*	Onagraceae
28. Compass plant, *Silphium laciniatum*	Asteraceae
29. Pasque flower, *Anemone patens*	Ranunculaceae

[1] dry site (Monona County) [2] mesic site (Story County)

Table 2. List of species from the thirty-species prairie mix that increased to some degree in Monona County plots with the second seed addition. Species in bold were completely absent in unseeded plots; all other species were already present to some degree in unseeded plots.

Original Treatment	Species increasing in abundance in seeded compared to unseeded plots
Spring, Mix Later	*A. tuberosa, H. helianthoides, S. scoparium, S. laciniatum, S. nutans, V. stricta*
Spring With Mix	*A. gerardii, D. purpurea, E. pallida, H. helianthoides,* ***L. capitata,*** *O. biennis, P. virgatum,* ***S. asper****, S. laciniatum, V. stricta*
Summer, Mix Later	*A. gerardii,* ***A. canadensis****, A. tuberosa,* ***E. pallida****, H. helianthoides, M. fistulosa,* ***S. asper****,* ***S. scoparium, S. nutans***
Summer With Mix	*H. helianthoides, M. fistulosa,* ***S. asper****, S. rigida, S. nutans, V. stricta*

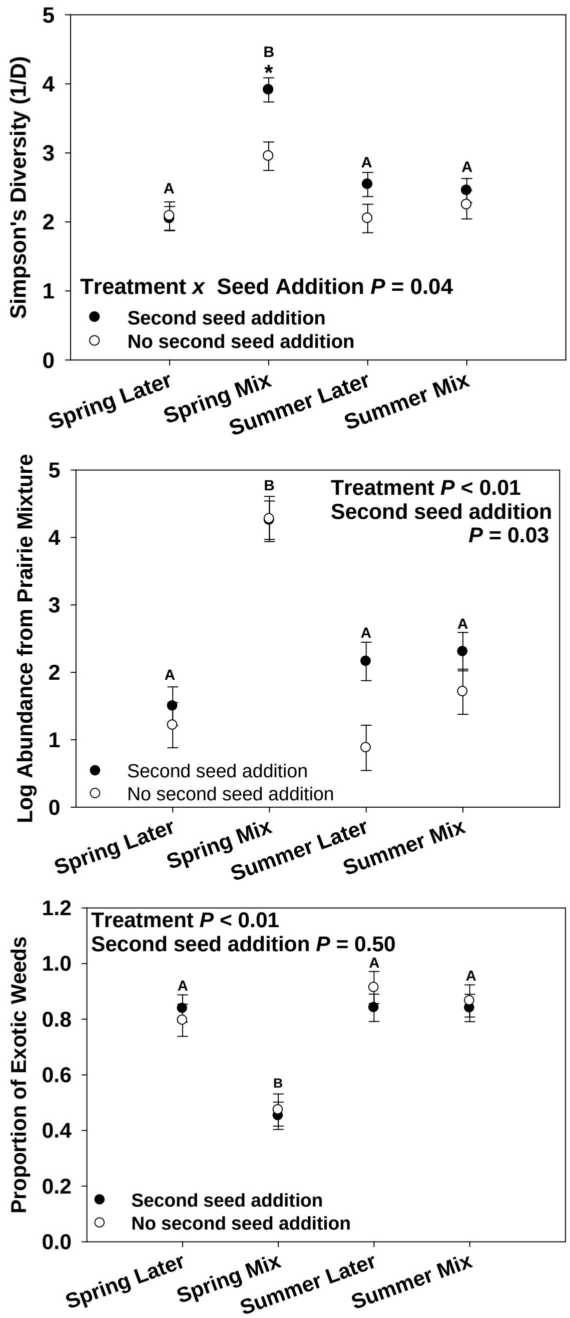

Figure 2. Mean Simpson's Diversity (top), abundance from mix (middle) and proportion of exotics (bottom) for all four treatments in Monona County plots in 2011. Points represent plots with no additional seed additions (open circles) and plots seeded a second time in spring 2011(black circles). Treatments were spring cover with mix seeded following spring, spring cover seeded with mix, summer cover with mix seeded following spring, summer cover seeded with mix. Treatment *P*-values and letters indicate significance among the four original treatments, and the asterisk indicates significant difference among seeded and non-seeded plots.

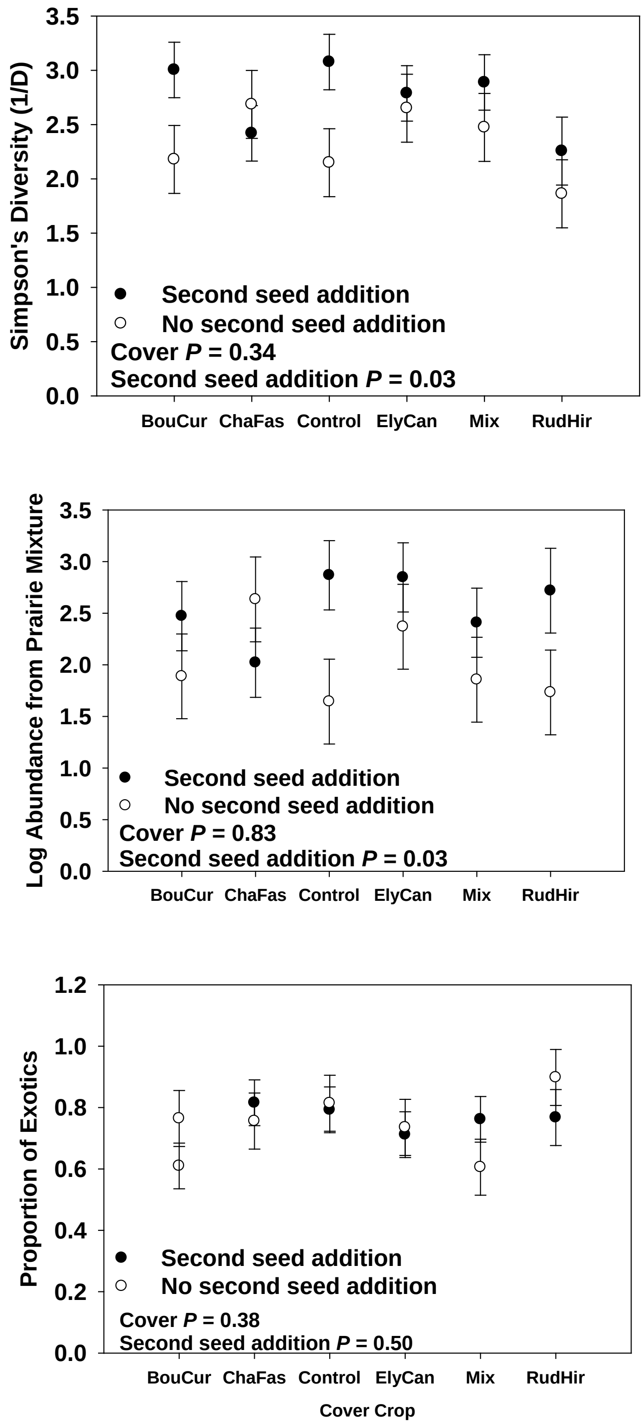

Figure 3. Relationships between cover crop species and Simpson's Diversity (top), abundance from the mix (middle) and proportion of exotic species (bottom), for plots with (black circles) and without (open circles) the second spring seed addition in Monona County, 2011.

Discussion and Conclusions

Altering timing of initial restoration seeding during the growing season (i.e. in the original experiment) so far appears to influence the outcome of prairie restoration communities more than altering identity of cover crops, or adding a second seed addition. We found previously that these original treatments produced diverse, native-dominated communities when they were seeded in the spring, but they produced low diversity, exotic-dominated communities when they were seeded in late summer, or a year after a cover crop was seeded (Martin and Wilsey, submitted). These treatments produced the same results at both the Story County and Monona County sites, and the communities have persisted for at least six years (Martin and Wilsey, submitted).

Overall, a second seed addition added to ash after a spring fire at Monona County plots increased both the abundance from the prairie mixture and diversity slightly in restoration plots that were established for seven years, but this increase was not large enough to converge the original treatments. Furthermore, adding more seeds did not reduce the proportion of exotics species. Therefore, differences were larger among the original treatments than they were between plots seeded a second time and non-seeded plots. Interestingly, diversity actually increased significantly with seed additions only in plots that already had the highest levels of diversity (i.e., those that were originally seeded in spring with the cover crop), suggesting perhaps that high diversity prairie plantings may be reinforced with seed additions, but it may be difficult to increase diversity with seed additions in plots dominated by exotic species.

Although the second seed addition had a minimal effect after the first year by increasing native species establishment and diversity, it did not lower weeds or converge communities, and consequently our results suggest that perhaps the most critical period for establishing native prairie restorations is during the early phase of establishment, i.e., the initial seeding. We previously found that in the more productive Story County plots, a second seeding in 2010 did not increase recruitment from the prairie mixture at all, nor did it increase diversity or lower exotic abundance (Martin and Wilsey 2010). There may be important differences between the Story County and Monona County sites that allowed some prairie species to establish with a second seed addition in one location but not the other, but even a second seeding in Monona County plots did not converge all prairie restoration plots to very high diversity and native species establishment as might be expected when more seeds are added. Importantly, once plants were established in restorations, overall it was more difficult to increase recruitment of prairie species, lower exotic species abundances, or increase diversity than establishing a successful restoration at the onset of the restoration process.

Overall, our results reiterate that 1) the timing of initial seeding is important to establishing a diverse and native-dominated restoration, 2) cover crops are not as effective as predicted over the long term for establishing prairie, and 3) over seeding prairie mixtures into established vegetation after a spring fire may not be an easy and efficient way to increase native recruitment and lower weedy species abundances. Other, more management intensive activities such as mowing or grazing, which were not done here, may be needed to reduce competition and increase recruitment in established restorations (Martin and Wilsey 2006, Williams et al. 2007). Therefore, focusing on establishing high levels of recruitment and diversity and excluding weedy species during a critical time early in establishment should be a priority for new restorations. Our results suggest adding mixes in the spring with no cover crop may be one way to accomplish this.

Literature cited

Jonasson, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52:101-106.

Martin, L.M., Moloney, K.A. and B.J. Wilsey. 2005. An assessment of grassland restoration success using species diversity components. Journal of Applied Ecology 42:327-336.

Martin, L.M. and B.J. Wilsey. 2006. Assessing grassland restoration success: relative roles of seed additions and native ungulate activities. Journal of Applied Ecology 43:1098-1109.

Martin, L.M. and B.J. Wilsey. 2010. Do fire and seed additions alter strong seed timing and priority effects on prairie establishment? IDOT Report.

Martin, L.M. and B.J. Wilsey. Submitted. Assembly history alters diversity, exotic-native proportions, and functioning of restored prairie plant communities.

Mlot, C. 1990. Restoring prairie. Bioscience 40:804-809.

Packard, S. and C.F. Mutel. 1997. The tallgrass prairie handbook: for prairies, savannas and woodlands. Island Press, Washington, D.C.

Polley, H.W., J.D. Derner, and B.J. Wilsey. 2005. Patterns of plant species diversity in remnant and restored tallgrass prairies. Restoration Ecology 13:480-487.

Shirley, S. 1994. Restoring the tallgrass prairie. An illustrated manual for Iowa and the Upper Midwest. University of Iowa Press, Iowa City.

Smith, D. 1998. Iowa Prairie: original extent and loss, preservation and recovery attempts. Journal of the Iowa Academy of Sciences 105:94-108.

Williams, D.W., Jackson, L.L., and D.D. Smith. 2007. Effects of frequent mowing on survival and persistence of forbs seeded into a species-poor grassland. Restoration Ecology 15:24-33.