# Using ecological theory to inform the restoration and conservation of tallgrass prairie

By

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# Abstract

Tallgrass prairie was once widespread in North America prior to European settlement, but now is almost entirely gone from the landscape. As a result, there has been a diligent effort to restore portions of land back to tallgrass prairie. However, these restorations often fall short of restoring the plant diversity and plant community composition seen in undisturbed prairies. In this dissertation, I use ideas in ecological theory to overcome two practical challenges practitioners face that diminish plant diversity in prairie restorations.

One potential reason that restored prairies often have lower diversity than undisturbed prairies is that undisturbed prairies exhibit an aggregated spatial structure that may enhance coexistence, while tallgrass prairie restorations have a uniform spatial structure that may encourage competitive exclusion. In chapter 1, I explore how the initial spatial structure of sown species affects the diversity and composition of the sown plant community, as well as the establishment of weeds in tallgrass prairie restorations. In this experiment, we manipulated the level of aggregation in experimental restorations and the functional similarity of aggregates. We found that the initial spatial arrangement of sown species substantially affects the outcome of restorations by altering the establishment of sown and non-sown species.

Invasive species are economically problematic and are suspected to be a leading cause of species extinction. Sericea, an invasive legume, is a particularly important invasive species in the Midwestern U.S. because of its potential to reduce to quality of grasslands. In chapter 2, I examine a large-scale data set from Fort Riley Military Reserve (FRMR) to determine if tallgrass prairie is intrinsically more resistant to Sericea invasion than disturbed grasslands, and to what degree human activity and propagule pressure affect the spread of Sericea across the landscape.

Results showed that tallgrass prairie is more resistant to Sericea than disturbed grasslands. We also found that human activities likely aid in Sericea’s invasion by disturbing the plant community and facilitating seed dispersal. Our findings enhance understanding of invasion ecology and the factors driving Sericea invasion.

In chapter 3, we sought to further refine our understanding of which characteristics of tallgrass prairies confer invasion resistance: the abundance of dominant, competitive species or their relatively high plant diversity. We also sought to explore the efficacy of adding tallgrass prairie restoration to existing Sericea management methods in controlling Sericea abundance on previously invaded land. In our restorations, we varied the methods used for site preparation, the density and diversity of seed mixes used, and the use of follow-up herbicide. We found that the site preparation used for restoration, the density of the seed mix, and the use of follow-up herbicide all affect the re-invasion of Sericea, but the diversity of the seed mix does not. Our results support the idea that dominant species are primarily responsible for conferring invasion resistance and demonstrate that incorporating tallgrass prairie restoration may be beneficial for Sericea management.

Overall, the results in the dissertation show that incorporating ecological theory into restoration practice is worthwhile. It not only advances our understanding of what regulates ecosystems, but can also improve the methods used in restoration practice, and ultimately improve our ability to restore degraded ecosystems.

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## Table of contents

## List of Figures

# List of Tables

# Introduction

Ecological restoration has likely been practiced for centuries as a way to maximize or reinstate valuable resources. However, using ecological restoration as a means to understand the mechanisms shaping ecosystems, restoration ecology, is relatively new. Perhaps the first recorded attempt to formally study the restoration process was conducted at the University of Wisconsin-Madison. In 1935, Aldo Leopold and others initiated a tallgrass prairie restoration with two main goals: to reestablish a small part of a disappearing ecosystem and to gain an understanding of how ecosystems function (Jordan et al., 1990). They envisioned this restoration as a means to ask questions and test basic ideas about plant communities' functions, how they change over time, and how they respond to disturbance (Leopold, 1934). Leopold and others were proposing a new field of ecology that develops theory to guide restoration and uses restoration to advance ecology; what would eventually be formalized as "restoration ecology" in the late 1980s (Aber and Jordan, 1985). Restoration ecology can be viewed as a subset of ecological theory that can be directly applied to the practice of restoring degraded ecosystems (ecological restoration). Integrating ecological theory into ecological restoration not only provides unique opportunities to test our understanding of ecological phenomenon, but also helps to prevent restorations from progressing solely by a series of trial and error improvisations. Despite widespread recognition of such reciprocal benefits, the integration of theory and restoration is inconsistent (Young 2005). Because practitioners often look to ecologists for practical guidance when conducting restorations, the lack of full integration hinders the success of restoration projects. This dissertation is an attempt to integrate ecological theory and the practice of restoring tallgrass prairies in hopes of advancing our understanding of the forces that regulate this ecosystem and providing guidance to restoration practitioners that can be used to improve restoration outcomes.

Despite considerable work being done to understand ecological dynamics within tallgrass prairie ecosystems, tallgrass prairie restorations often have lower plant diversity and forb abundance compared to undisturbed prairies (Kindscher 1994). Two features of restorations that contribute to their relatively low diversity are the tendency of restorations to become dominated by a few aggressive native species (tallgrasses) that exclude others (Sluis 2002, Camill et al. 2004) and exotic species invasions that reduce plant diversity (Briggs et al. 2002, Brandon et al. 2004, Reed et al. 2005). Both features are similar in that over time, one or a few species can dominate the plant community at the expense of other species. Determining factors/mechanisms that influence species' abundances within communities is at the heart of coexistence theory. Applying ideas within coexistence theory to tallgrass prairie restoration could lead to improved methodologies for enhancing native diversity. In this dissertation, I use ideas within coexistence theory as a foundation from which to make and test predictions about the outcomes of plant interaction in tallgrass prairie communities relevant to the two issues mentioned above. The following paragraphs outline the practical motivations for each chapter, the theory underlying the design of each study, and the brief summary of the results.

### *Chapter 1. Initial spatial structure alters diversity and community composition of a tallgrass prairie restoration.*

Establishing and maintaining native plant diversity is a common challenge in tallgrass prairie restorations. Many restorations gradually become dominated by a few aggressive plant species accompanied by a precipitous loss of more rare plant species over time (Sluis 2002, Camill et al. 2004). The relatively low diversity of tallgrass prairie restorations likely results from a number of factors that historically maintained plant diversity including the lack of keystone herbivores (Knapp et al. 1999), alteration of soil mutualists (Bauer et al. 2015), changes in disturbance regimes (Howe 1994), or the limited diversity of restoration seed mixes. The relatively low diversity of restoration may also be influenced by current methods used for sowing native seed. Typically, seed mixes are often homogenized and sown uniformly across restorations. This uniform spatial structure of restored communities may deviate from a more aggregated spatial structure found in remnant prairies (Polley et al. 2005). Spatial coexistence theory predicts that species aggregation will mediate interaction and promote coexistence by relaxing inter-specific competition for shared resources. We can extend this idea into the arrangement of species within prairie restorations. If there are competitive differences between species in the community, uniformly sowing species throughout the community initially will promote competitive exclusion, but aggregated communities will maintain diversity by limiting interactions between competitively disparate species. However, it is not clear which species are excluding others. Chesson (2000) suggested that stabilizing forces such as pathogens or herbivores (which can enable coexistence) may limit the suppressive effects of dominant species such as $C_4$ grasses by reducing their vigor. Alternatively, Chesson also suggested that equalizing forces such as niche partitioning may enable coexistence by relieving competition for shared resources. We sought to determine to what degree these two mechanisms may be regulating coexistence and determine how spatial aggregation affects the outcome of species interactions early in restoration. To do this, we examined the abundance, diversity, and composition of sown and non-sown (weed) species in experimental restorations that varied in their level of initial spatial aggregation.

In chapter 1, my aim is to evaluate aspects of spatial coexistence theory while also assessing the potential utility of spatial planting strategies for tallgrass prairie restorations. We established replicate prairie restorations that were identical in composition of sown species, but varied in initial spatial arrangement at sowing. Across each restoration plot, species were either sown uniformly, aggregated into monospecific patches, or aggregated into patches with species subsets that were functionally similar, functionally different, or random with respect to functional group designation. The results from chapter 1 show strong effects of initial aggregation on the abundance of dominant sown prairie species, the emergent weed community, and overall community composition, but inconsequential effects on species diversity at this early stage. Generally, as spatial aggregation declined among our treatments, we saw significant increases in the abundance of 5 of the 16 species. In uniformly sown restorations, (similar to what is done in most restorations) a few aggressive species covered were very abundant, and weed abundance was relatively low; indicating that spatial structure appears to affect community composition by altering interactions among fast growing species and weeds at the early dynamic stages of restoration.

### *Chapter 2. Are native tallgrass prairies more resistant to invasion than abandoned cropland? A landscape-scale study of Lespedeza cuneata*

It is well established that invasive species are ecologically and economically problematic (Pimental et al. 2005). To limit the spread of invasive species and minimize their future impacts, research has focused on understanding what types of communities are more resistant to invasion. If some communities are inherently more resistant to invasion, an understanding as to why may make it possible to restore or create communities that are resistant to invasion. Observational studies that examine the spread of invasive species into different communities at large scales are often unable to account for other factors that also influence invasion such as propagule pressure and disturbance (Williamson 1996, Lonsdale 1999, Hierro et al. 2005). The aim of this chapter is to advance our knowledge of the general factors governing invasion by examining the spread of an exotic invasive of particular interest in the Midwestern U.S.:*Lespedeza cuneata* (Sericea). Sericea is an herbaceous legume that originated in Asia and was introduced into the U.S. in the early 1900's. Sericea has invaded vast areas of grasslands in the Midwest where it reduces the diversity of native communities and causes losses of forage production in rangelands (Fechter and Jones 2001). The goals of this chapter are: 1) to determine if there are intrinsic differences in the invasion resistance of abandoned cropland and native tallgrass prairie; 2) to understand if human-aided dispersal and disturbance contribute to the spread of Sericea; and 3) understand the relative contributions of these factors.

To do this, we first examine the degree to which military activity, grassland type, and propagule pressure affect the spread of Sericea across a 40,000 hectare landscape at Ft. Riley Military Reserve (FRMR) using spatial modeling and variance partitioning analysis. We also compare observed levels of Sericea invasion into tallgrass prairie and abandoned cropland to a series of null models of invasion that simulate invasion that assume no differences in invasion rates. We found that after controlling for the propagule pressure and disturbance, tallgrass prairie is more resistant to Sericea invasion than abandoned cropland and the distribution of Sericea invasion at FRMR largely reflects the distribution of military activity and the distribution of the two grassland types. We also found that Sericea invasion is likely promoted by human facilitated seed dispersal.

### *Chapter 3: Restoring Land Heavily Invaded by Sericea Lespedeza (Lespedeza cuneata): testing hypotheses within community invasibility theory*

After a site has been invaded by Sericea, it is necessary to repeatedly treat Sericea plants with herbicide to prevent re-invasion. There is some evidence that restoring sites to native tallgrass prairie increases their resistance to Sericea invasion (Foster et al. 2015). Chapter 2 provided additional support for this by showing lower rates of Sericea invasion into tallgrass prairies at the landscape scale. However, it is unclear what attributes of the restored community confer invasion resistance. It is also unclear if restoration can be used on previously invaded sites to reduce both the re-invasion of Sericea and the need for ongoing management.

Classic ecological theory predicts that more diverse plant communities will resist invasion (Elton 1958). While experimental studies have found that invasion resistance is associated with high plant diversity (Tilman 1997, Naeem 2000, Kennedy et al. 2002), there is evidence that this effect may often be due to the influence of highly abundant and competitive species (Wardle 2001, Smith et al. 2004). Before restoration can be used as a tool to enhance the resistance of plant communities to exotic invasion, we must know what attributes to restore. Furthermore, it is unclear what methods should be used to minimize invasion or if restoration can reduce the abundance of invasive species in areas previously invaded. The aim of this chapter is to advance our understanding of invasion ecology and improve Sericea management in grasslands invaded by this species

We conducted a series of experimental tallgrass prairie restorations in an abandoned hayfield previously invaded by Sericea in eastern Kansas. This experiment was designed to understand the importance of two attributes thought to contribute to the invasion resistance generally and perhaps the invasion resistance observed in tallgrass prairie: plant diversity and the abundance of dominant species. Both are thought to increase invasion resistance by reducing resource availability. We first prepared restoration plots with herbicide only or with herbicide and soil tillage. Then we broadcasted native seed mixes that varied in diversity and density to create differences in plant diversity and the abundance of dominant species. Then, a subset of the restoration received a follow-up herbicide treatment that targeted Sericea plants. Our results showed that Sericea was negatively affected by higher density seed mixes, but not higher diversity ones. Additionally, preparing the restoration site with mechanical tillage is more effective at reducing Sericea re-invasion compared to only preparing sites with herbicide. When tallgrass prairie restoration is combined with follow-up herbicide application, two growing seasons after restorations were conducted, Sericea levels are very low to non-existent and native cover is high. However, we cannot know whether this low level of Sericea abundance will persist. Generally, our results suggest that native tallgrass prairie can establish successfully in heavily invaded areas, and even without follow-up herbicide application, Sericea abundance is lower than prior to restoration.

The results from these three chapters demonstrate that that the application of ecological theory to questions in ecological restoration can both advance our understanding of ecological theory and improve our ability to restore degraded ecosystems. My hope is that this dissertation fosters a diligent effort to integrate the two fields.

# Chapter1

## Initial spatial structure alters weed abundance and sown community composition of a tallgrass prairie restoration.

## Abstract

Understanding the mechanisms that regulate species coexistence within communities remains a central goal in ecology that has important implications for the conservation and restoration. Establishing and maintaining native plant diversity is a common challenge when restoring communities that may be addressed by using principals in coexistence theory. Here, we evaluate aspects of spatial coexistence theory while assessing the potential utility of spatial planting strategies for tallgrass prairie restoration by sowing replicate prairie restorations that vary in the initial spatial arrangement of sown species. Replicate prairie restorations were identical in composition of sown species, but varied in spatial arrangement. Across each restoration plots, species were either sown uniformly, aggregated into monospecific patches, or aggregated into patches with species subsets that were functionally similar, functionally different, or random. Results show strong effects of initial aggregation on the abundance of dominant sown prairie species, the emergent weed community, and overall sown community composition, but inconsequential effects on species diversity, richness, and evenness. Decreasing spatial aggregation disproportionately favored the growth of dominant species which suppressed weed growth, but not subordinate forb growth. We found no difference in community composition, diversity, evenness, or sown species abundance between restorations that aggregated functionally similar or functionally dissimilar species. In prairie restorations and perhaps early succession in general, spatial structure which alters the functional similarity of interacting species largely does not affect community dynamics. Instead, spatial structure appears to affect community composition by altering interactions among fast growing species and weeds.

## Introduction

Understanding the mechanisms that regulate species coexistence within communities remains a central goal in ecology that has important implications for the conservation and restoration of native plant communities. Establishing and maintaining native plant diversity is a common challenge when restoring communities—a challenge that may be addressed by using principals in coexistence theory to improve restoration outcomes. Chesson (2000) proposed a framework for understanding coexistence that may help guide restoration practice. In his framework, species coexistence is determined by the balance of fitness differences among species (differential growth and reproduction) that promote exclusion, and stabilizing/equalizing mechanisms that reduce the intensity and asymmetry of competitive interactions, respectively. If fitness differences exist between interacting species, there must also be stabilizing and/or equalizing forces of equal or greater magnitude to allow stable coexistence. Equalizing forces are often thought of as interactions which negatively affect species with fitness advantages, such as selective herbivory or host specific pathogens. These limit the growth of relatively fit species and limit their ability to exclude less fit species, promoting coexistence. Niche partitioning and intra-specific spatial aggregation (stabilizing forces) may both contribute to coexistence by increasing the relative strengths of intra- relative to inter-specific competition, an important condition for stable coexistence (Gause 1934). However, there is a subtle but important difference between niche partitioning and spatial aggregation. Niche partitioning reduces competition between interacting species by reducing overlap in resource utilization between species (MacArthur and Levins 1967). Since all plants within a community share some vital resources (nutrients, light, and water), niche partitioning may not be sufficient to prevent exclusion between species with large fitness differences. Spatial aggregation could be more effective at allowing coexistence between any two plant species because individual plants compete most strongly with close neighbors (Harper 1977, Goldberg 1987, Pacala and Silander 1990). Given enough distance, individuals within species aggregates will experience very weak interactions with other species. In natural plant communities, spatial aggregates of plant species produced by endogenous processes (limited dispersal, clonal growth etc.) may be an important factor that reduces competition between species and enables coexistence (Polley et al 2005, Dale and Powell 1994, Kershaw 1958).

Several experimental studies have been conducted that explore the effects of spatial aggregation on plant species interactions. For the most part, these studies report results consistent with the hypothesis that intra-specific aggregation promotes coexistence by preventing or slowing competitive exclusion in plant communities (Stoll and Prati 2001, Yurkonis and McKenna 2014, Porensky et al 2012). However, these studies are typically conducted with only a few species, at small scales, and under controlled settings. Because of these artificial conditions, we cannot anticipate the effects of spatial structure when it is incorporated into diverse plant communities. In this study we present initial results of a long-term tallgrass prairie restoration experiment to evaluate the effects of initial species and functional group aggregation on native prairie species establishment and persistence. We investigate alternative mechanisms of coexistence and evaluate alternative spatial sowing strategies for enhancing prairie species establishment and diversity.

If spatial structure is important to coexistence and the maintenance of diversity, could the purposeful introduction of spatial structure at the sowing stage of restoration enhance the establishment, persistence and diversity of desired species, and this improve restoration success? In this study, we evaluate the effects of spatial aggregation in the context of prairie restorations initiated on abandoned cropland on sown species diversity, community composition, and weed establishment. Restoring high diversity prairie communities has proven difficult in large part to the difficulty of establishing forb species (non-grasses), which make up the majority of plant species in tallgrass prairies (Collins et al.1998, Kindscher 1994). There are likely numerous reasons for low forb abundance and diversity in prairie restorations, such as the lack of seed availability, lack of keystone herbivores (Knapp et al. 1999), and altered soil mutualisms (Hartnett and Wilson 1999). Another prevalent hypothesis is that the highly competitive and often aggressive native $C_4$ grasses suppress native forb species (Packard and Mutel1997, Weber 1999, Kindscher and Fraser 2000, Dickson and Busby 2009).

The suppression of native forbs by the dominant native grasses in prairie restorations may be partially explained by the relatively high seed densities of grasses used in many restorations (Dickson and Busby 2009, Kindscher and Fraser 2000). However, another possibility is that the common practice of planting species uniformly throughout restoration (Packard and Mutel 1997) may limit opportunities for forbs to avoid competition with grasses via spatial segregation. If intraspecific aggregation is important to coexistence, is it possible that uniform sowing strategies may be detrimental to the establishment and persistence of desired species? Uniform sowing strategies may expedite competitive exclusion in restorations by maximizing inter-specific, relative to intra-specific interactions within local patches, minimizing the stabilizing effects associated with patchy species distributions. If this is the case, sowing strategies that introduce spatial structure into prairie restorations may enhance coexistence or at least slow the exclusion of desired species (Rees et al. 1996, Gram et al. 2004) by inhibiting the growth of competitively superior species and enhancing the growth of competitively inferior ones (Stoll and Prati 2001, Wassmuth et al. 2009, Houseman 2013, Yurkonis and McKenna 2014, Porensky el al. 2012).

If coexistence of species within restorations can be enhanced by introducing patchy spatial structure, one question must be answered before it can be implemented at larger scales: How should large numbers of plant species of varying fitness and functional niche similarity be sown spatially within restorations to maximize establishment and persistence? If the stabilizing effect of niche differences is the most important factor limiting exclusion and permitting coexistence in a developing restoration, sowing strategies that spatially segregate functionally similar species but aggregate functionally different (complementary) species may be most beneficial. On the other hand, if large fitness differences between functional groups overwhelm the stabilizing effects of niche differences, then sowing strategies that spatially segregate functional groups with large fitness differences may be more effective. If this is true, sowing restorations in a way that segregates a dominant, high-fitness functional group (such as native grasses) from a subordinate functional group (forbs) may be more effective in minimizing forb exclusion than segregating species within the same functional group.

However, introducing spatial structure into restorations may exacerbate the establishment of non-sown species that constrain the successful establishment of prairie species (Packard and Mutel 1997). Uniform planting has been promoted in the past as a way to control weeds in prairie restorations by assuring widespread coverage of highly competitive $C_4$ grasses (Schramm 1990, Betz 1996). A spatial planting strategy that segregates native forbs from native grasses may create a Catch-22 situation where forbs are exposed to suppression by weeds, which have themselves benefited from the spatial segregation from native $C_4$ grasses. If one creates spatial structure in a restoration, how does the potential benefit of spatially segregating forbs from competition with grasses weigh against the detriments of their exposure to weed suppression?

In this field experiment, we investigate the effects of initial species aggregation on community structure by sowing replicate restoration plots to five different spatial configurations. All restoration plots were sown with the same sixteen species at equal densities, varying only the extent of species and functional group aggregation among patches within each plot. Treatments ranged from plots where at one extreme, the sixteen species were sown into monospecific patches (one species per patch; high initial intra-specific aggregation) to plots where species were uniformly sown (low intra-specific aggregation). Three intermediate aggregation treatments were employed (four species per patch), which varied the extent of inter-specific functional similarity of sown species competing within local patches.

We present the first results from this experiment and document plant community responses measured in the fourth growing season after sowing. The findings reported here are most relevant to the initial establishment stages of restoration. Future work will address long-term dynamics as the study matures. We address the following questions:

1) Does initial spatial aggregation of sown species affect early prairie species establishment, abundance, diversity and species composition at the whole community scale (plot-scale); and, does it alter the abundance of undesired non-sown species (weeds)?

2) To what extent are any effects of aggregation on the developing community mediated by interactions among sown prairie species versus interactions between sown species and emergent weeds?

3) If interactions among the sown prairie plants are important, what spatial arrangement leads to the greatest establishment success and diversity of prairie species at the whole-community scale: where functionally different species or functionally similar species are aggregated together?

If niche differences among competing species in close proximity within patches are most crucial for coexistence, we predict the former. If the minimization of fitness differences among closely competing species is most crucial for coexistence we predict the latter.

## Methods

### *Study site*

This study was initiated at the University of Kansas Field Station (KUFS) operated by the Kansas Biological Survey at the University of Kansas (KU) in northeastern Kansas (lat 30°03’N, long 95°12’W). This area of Kansas is within the prairie-forest ecotone region of the Midwest. The experimental field site at KUFS was previously utilized for row crop agriculture and later converted into cool-season hay management. The site was fertilized (1985-1987) and hayed, (1985-1988) and periodically grazed by cattle before 1990. From 1995-2000, the site received no management. Since 2000, KUFS has maintained the site by spraying exotic invasive species with herbicide and periodically mowing and burning the site. Prior to the establishment of this experiment, the study site consisted mainly of exotic, $C_3$ grasses: smooth brome (*Bromis inermis* Leyss), tall fescue (*Schedonorus arundinaceus* (Schreb.) Dumort. nom. cons.), Kentucky bluegrass (*Poa pratensis* L.), along with broomsedge (*Andropogon virginicus* L.), an opportunistic native $C_4$ grass.

### *Experimental design*

In the early spring of 2011, a 5 x 5 grid of 25 10x10-m plots was established at the site, following a randomized blocked design. Four meter buffer strips included between restoration plots where no native plant species were seeded. The entire site was burned to remove dead vegetation. Then, when vegetation began to regrow, the site was sprayed with herbicide and raked to scarify the soil to improve seed germination. Each plot, which is a single replicate prairie restoration, was divided into 16, 2.5 x 2.5-m patches (Figure 1.1). Sixteen common prairie plant species were seeded into all restoration plots in equal densities, but the spatial arrangement of the species was varied according to one of five spatial planting treatments (n = 5; Figure 1.2). The spatial structure of each treatment was altered by distributing the seeds of each of the sixteen species into one, four, or all sixteen patches within each restoration. The particular combination of species that were included in a given patch was chosen in order to vary the amount of initial intra-specific spatial aggregation and level of functional similarity of interacting species in each treatment. At one extreme, we seeded restoration plots with a uniform spatial structure by planting all patches with all 16 species (consistent with typical restoration) to minimize intraspecific aggregation and to maximize interspecific encounters between species within patches (UNIFORM treatment). At the other extreme, seeds were sown into highly spatially aggregated patches by seeding each of the 16 patches to a single species; maximizing species aggregation and minimizing interspecific encounters within patches (AGMON treatment). The other three treatments (AGCOM, AGRED, AGRAN; Figure 1.2) aggregated four-species combinations into each patch of a plot to create an intermediate level of spatial aggregation, but varied the amount of functional similarity between the aggregated species sown to each patch. Each of the 16 species was classified into one of four broad plant functional groups ($C_4$ grass, tall forb, short forb, legume; Table 1.1) determined by differences in metabolic pathway ($C_3$ or $C_4$), average mature height, and their ability to fix nitrogen (legume or not). The majority of the species present in native tallgrass prairies fell into one of these four functional groups. Patches within restorations belonging to the AGRED (aggregated redundant species) treatment contained all four species of a functional group, maximizing functional similarity of interacting plants. The

AGCOM (aggregated complimentary species) treatment minimized functional similarity by sowing one species from each of the four functional groups in each patch. The AGRAN (aggregated random species) treatment produced intermediate levels of functional similarity by sowing four randomly chosen species from the pool of 16 species into each patch.

*Seed sowing and data collection*

Native plant seeds were purchased from three seed suppliers (Stock Seed Farms, Murdock, NE, U.S.A.; Missouri Wildflowers, Jefferson City, MO, U.S.A.; and Agrecol, Janesville, WI, U.S.A.). Early in 2011, we performed germination tests for each species to control for differences in seed viability and to ensure that the number of viable seeds was held as constant as possible for all species. In March of 2011, the perimeter of the experiment was measured and the site was burned to remove the previous season's dormant vegetation. After regrowth appeared, the site was sprayed with herbicide and raked to remove dead vegetation. Restoration plots were marked leaving a 4m buffer strip between each plot. In April of 2011, seeds were sown at a rate of 200 viable seeds/m² by hand broadcasting soil was scarified with rakes and then lightly tamped to improve germination. Due to very poor germination, we seeded the experiment a second time in the winter of 2012. Restoration plots were burned every spring since 2011 (prior to plant growth) to remove litter accumulation from non-sown species the previous year.

Here, we present the results of vegetation surveys conducted in July of 2014 (the fourth growing season of the experiment). We performed percent cover surveys in each of the 400 patches in the experiment (16 patches per plot x 25 plots). Cover surveys were performed by centering a one m² quadrat in the middle of each 2.5 x 2.5-m patch. Percent cover values were assigned to all sown and non-sown species in each patch, allowing total cover values to exceed 100% to account for the biomass in multiple levels of the plant canopy. In order to determine how different components of the plant community influences light availability, photosynthetically active radiation (PAR) at soil surface (percentage of PAR penetration) were measured in all 400 patches in the experiment in August 2014 using a 0.8m PAR ceptometer (Decagon Devices, Pullman, Washington, USA).

### *Data Analysis*

For these analyses, we combined the cover values for all plant species not included in the original 16 sown species into one value "non-sown species" which included non-sown grasses and non-sown forbs. Most non-sown cover consisted of dogbane (*Apocynum cannabinum* L.), Canada golden rod (*Solidago Canadensis* L.), and tick-trefoil (*Desmodium sp.*), but also included very small amounts of several desirable tallgrass prairie species that likely contaminated our seed mixes. Sown prairie "forbs" included all leguminous and non-leguminous dicot species included in experimental sowing treatments. When needed, we distinguish between the two groups by specifying either "legumes" or "non-leguminous forbs". The cover values used for our analyses were averaged across all 16 cells in each restoration plot to illustrate differences in species abundances at the plot scale.

Richness ($S'$), the exponential of Shannon diversity ($e^{H'}$), and Evenness ($H'/\ln S'$) were calculated using only sown species cover to evaluate the effects of the spatial treatments on sown community diversity. These diversity indices were calculated using cover values averaged across all 16 cells within plots. To evaluate the success of establishing the initial spatial structure within plots as intended by the experimental treatments, beta-diversity was calculated by using the mean

Bray-Curtis dissimilarity between all pairwise combinations of patches for each restoration plot. An ANOVA was then performed on the mean Bray-Curtis dissimilarities to determine statistical significance between treatments.

One-way ANOVAs were used to evaluate the effects of spatial aggregation treatments on the exponent of Shannon diversity, total sown species cover, total non-sown species cover, absolute functional group cover, and cover of individual species. Species richness was not tested because of little variation among treatments and could not be statistically evaluated. A block term was included in all ANOVAs which tested for the effects of spatial treatments. The Shapiro-Wilk test and Bartlett test were used to confirm the assumptions of ANOVA. No transformations were needed for response variables. Tukey pairwise comparisons were performed to determine differences in Shannon diversity, total sown cover, total non-sown cover, and the absolute abundances of the tall forb and $C_4$ grass functional groups between all pairwise combinations of our spatial treatments. The absolute abundances of *Sorghastrum nutans* (L.) Nash and *Ratibita pinnata* (Vent.) Barnhart did not meet the assumptions of ANOVA, so we tested for potential differences among our treatments using Friedmans's rank tests which included a blocking term.

Non-metric multidimensional scaling (NMDS) utilizing Bray-Curtis dissimilarity index was used to ordinate restoration plots and to evaluate variation in community composition based on the relative cover values of constituent sown species. No transformations were performed on relative sown species abundances. Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used to evaluate the statistical significance of treatments on the relative species cover values and relative functional group cover of the sown plant communities. PERMDISP tests of homogeneity of dispersion were used to detect differences in multivariate dispersion between treatment groups.

Comparisons of the absolute abundances of the different sown species in patches within the AGMON treatment were done to determine which of our sown species' abundances are limited by available space in aggregates and which are potentially limited by interspecific interactions, we compared the cover values of each sown species in their respective patches with AGMON plots. To determine if the absolute abundance of individual species differed from each other in patches where they had been planted alone, we performed a one-way ANOVA. The Shapiro-Wilk test and Bartlett test were used to confirm the assumptions of ANOVA. All statistical analysis was performed in the R software version 3.0.2 and utilizing the "vegan" package. Figures were made using "ggplot2" package in R.

## Results

### *Treatment Establishment*

As intended by the experimental design, spatial treatments altered initial patterns of intra-specific aggregation of sown species within restoration communities in the fourth growing season, as illustrated by significant treatment effects among-patch compositional dissimilarity (within community beta-diversity; $F_{4,19} = 511$, $P < 0.001$) (Figure 1.3a). The UNIFORM and AGMON treatments exhibited the highest and lowest levels of compositional dissimilarity respectively, while the intermediate aggregation treatments, (AGCOM, AGRAN, and AGRED) exhibited intermediate levels of dissimilarity.

### *Diversity and vegetation cover*

Sown species richness did not vary significantly among the treatments (Figure 1.3b). The exponential of Shannon diversity for sown species was significantly lower in the UNIFORM treatment compared to the AGMON treatment (Figure 1.3c; $F_{4,19} = 3.2$, $P = 0.038$). There were no significant differences among the AGCOM, AGRED and AGRAND treatments. Spatial aggregation significantly affected sown species Evenness (Figure 1.3d; $F_{4,19} = 4$, $P = 0.015$). AGRED and UNIFORM treatments both had significantly lower Evenness than the AGMON treatment ($P < 0.05$, $P < 0.05$), but the AGCOM, AGRED and AGRAN treatments were not significantly different.

Total cover of sown species was significantly different between treatments ($F_{4,19} = 17.9$, $P < 0.001$) and decreased as the level of intra-specific aggregation increased ranging from the highest of 86% in the UNIFORM treatment to a low of 32% in the AGMON treatment (Figure 1.4a). Sown cover in the UNIFORM treatment was significantly higher than all other treatments and the AGMON treatment had lower cover than all other treatments except for the AGRED treatment (Figure 1.4a). There was a trend of increasing total sown cover as functional aggregation decreased in the AGRED, AGRAN, and AGCOM treatments, but these differences were not significant. Non-sown species cover was also significantly different between groups ($F_{4,19} = 5.3$, $P < 0.005$) and decreased as functional group aggregation declined. The two most aggregated treatments (AGMON and AGRED) had significantly more non-sown cover than the two least aggregated treatments (AGCOM and UNIIFORM) and the AGRAN treatment had an intermediate level of non-sown cover. There were no significant differences in non-sown cover among the AGRED, AGRAN, and AGCOM treatments. Despite treatment effects on non-sown and sown species cover, there were no significant differences in total vegetation cover (sown plus non-sown) among treatments ($F_{4,19} = 1.5$, $P = 0.24$).

### *Sown Species Community Composition*

*Absolute cover*: The absolute cover of sown species within the tall forb and $C_4$ grass functional groups differed significantly among our treatments, but the absolute cover of short forb and legume groups did not (Figure 1.4b; $F_{4,19} = 12.6$, $P < 0.001$; $F_{4,19} = 11.2$, $P < 0.001$; $F_{4,19} = 1.3$, $P = 0.3$; $F_{4,19} = 0.7$, $P < 0.5$; respectively). Sown species within the tall forb and grass functional groups comprised the majority of cover across all treatments with mean absolute covers of 19% and 30% respectively. Sown species within the short forb and legume functional groups were less abundant in all treatments with mean absolute covers of 1% and 3% respectively (Figure 1.4b). Generally, as aggregation decreased, the cover of tall forbs and $C_4$ grass increased. In both groups, there were large differences between the AGMON and UNIFORM treatments. There were no statistical differences in tall forb cover among intermediate aggregation treatments, but grass cover was significantly greater in the AGCOM treatment compared to the AGRED treatment.

*Relative cover*: $C_4$ grasses composed the largest portion of the sown species community in every spatial treatment averaging 53.3% relative cover across all treatments, followed by tall forbs with 35.1% cover, and short forbs and legumes with 5.4% and 5.6% covers respectively. Despite only two of the four functional groups showing significant differences in absolute cover, there was no significant difference in sown community composition based on relative cover of functional groups (PERMANOVA, $P = 0.191$; PERMDISP, $P = 0.39$ ). Although treatments did not differ in relative functional group composition, the treatments did significantly alter sown species community composition based on their relative abundances (PERMANOVA, F = 2.7, $P = 0.001$, Figure 1.5). Pairwise analysis of treatments showed significant compositional difference between the UNIFORM and AGMON treatments (F = 3.8, $P = 0.008$) and also between the UNIFORM and AGRED treatments (F = 3.6, $P = 0.007$). The AGCOM, AGRED and AGRAN treatments were not significantly different. A test for the assumption of multivariate homogeneity of dispersion (PERMDISP) showed that the UNIFORM treatment had significantly lower dispersion among replicate plots than the AGMON and AGRED treatments (*P* = 0.016, *P* = 0.041). The NMDS ordination; Figure 1.5) showed that when making visual comparisons between the UNIFORM and AGMON treatments and UNIFORM and AGRED treatments, there were differences in both the dispersion and a centroid shift between these groups indicating that the significant difference between the AGRED and UNIFORM and also the AGRED and UNIFORM treatments could not be entirely attributed to differences in dispersion.

*Individual Sown Species Responses*

Differences in relative community composition of sown species primarily reflected significant differences in the absolute cover of two grass species *Sorghastrum nutans* (*S. nutans*) and *Schizachyrium scoparium* (Michx. Nash; *S. scoparium*) ($F_{4,\,19} = 37.9$, $P < 0.001$; $X^2 = 13.4$, df = 4, $P < 0.01$; respectively) and three less dominant, but common forb species *Heliopsis helianthoides* (L.) Sweet (*H. helianthoides*), *Monarda fistulosa* (L.; *M. fistulosa*), and *R. pinnata* in the tall forb functional group ($F_{4,\,19} = 14.4$, $P < 0.001$; $F_{4,\,19} = 4.1$, $P < 0.05$; $F_{4,\,19} = 8.8$, $P < 0.001$; respectively, Figure 1.6). Compositional differences between the AGCOM and UNIFORM treatments resulted primarily from a nearly four-fold higher absolute cover of *R. pinnata* (tall forb), a nearly five-fold higher absolute cover of *S. nutans* (grass), and modestly higher absolute cover of *H. helianthoides* (tall forb) and *S. scoparium* (grass) and *M. fistulosa* (Figure 1.a and e) in the UNIFORM treatment.

Sown community compositional differences between the AGRED and UNIFORM treatments were more subtle than between the AGCOM and UNIFORM treatments. Overall, sown species in the AGRED treatment had lower absolute cover than in the UNIFORM treatment. However, *H. helianthoides*, *M. fistulosa,* and *S. scoparium* had disproportionately lower absolute covers compared to the two dominate species and actually had a lower mean absolute cover than in the AGMON treatment. The absolute cover of *S. nutans* and *R. pinnata* were both lower in the AGRED treatment than in the UNIFORM treatment, but *S. nutans* had a lower absolute cover than *R. pinnata;* the only instance in all of the treatments (Figure 1.b). The relative sown community composition of the AGRAN and AGCOM treatments did not significantly differ from that of the other three treatments.

We compared the absolute abundance of sown species within monospecific patches within the AGMON treatment and found that there is a significant different among individual sown species ($F_{15, 64} = 9.7$, $P < 0.001$). While we did not conduct pairwise comparisons between individual species, qualitatively they fell into three general levels of abundance (Figure 1.7). *Andropogon gerardii* (*Vitman*)*, S. nutans, R. pinnata*, and *S. scoparium* had relatively high absolute abundances. *Echinacea pallida* (Nutt.) Nutt.*, H. helianthoides, Lespedeza capitata* (Michx.)*, Panicum virgatum* (L.)*, Helianthus maximiliani* (Schrad.), and *M. fistulosa* have intermediate absolute abundances. *Penstemon digitalis* (Nutt. ex Sims)*, Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald*, Dalea purpurea* (Vent.)*, Coreopsis lanceolata* (L.), and C*oreopsis palmate* (Nutt.) have low absolute abundances.

## Discussion

The goal of this experiment is to evaluate the effects of initial spatial structure on the establishment and persistence of sown prairie species and on long-term species coexistence and diversity. In doing so, the aim is to evaluate aspects of spatial coexistence theory while also assessing the potential utility of contrasting spatial planting strategies for community restoration.

Here we present the first results of this experiment, documenting treatment effects early on in community development. Future work will report long-term results as the experiment matures. Results to date reveal strong effects of initial species and functional group aggregation on the abundance of dominant sown prairie species, the emergent weed community and overall community composition, but inconsequential effects on species diversity at this early stage. Below I discuss the nature of these results in light of spatial coexistence theory, Chesson's coexistence model, and in the context of early stages of community development. Then I discuss implications of the findings for prairie restoration.

Basic spatial theory predicts that intra-specific spatial aggregation will promote coexistence and diversity by reducing intraspecific interactions. In this case, the establishment of prairie species and species diversity should be greater in the AGMON versus UNIFORM treatment. We found that as aggregation decreased among our treatments, two aggressive sown species with high fitness (*S. nutans*, *R. pinnata*) within the $C_4$ grass and tall forb functional groups greatly increased in abundance, resulting in a large difference in total sown species abundance between the AGMON and UNIFORM treatment. The disproportional increase of a few species within the $C_4$ grass and tall forb functional groups shifted relative sown community composition toward those fast growing species which slightly decreased sown species diversity and evenness. Also, the variability in community composition at the plot scale was lower in monospecifically aggregated restorations than in uniform ones. Because the relative abundances of dominant species was much lower in the AGMON treatment, small fluctuations in the abundance of less dominant species have a larger impact on relative species composition in the AGMON treatment than they do in the UNIFORM treatment.

Spatial coexistence theory predicts lower diversity in uniformly structured communities due to the exclusion of less competitive species. Among our spatial treatments, less aggregated spatial structure did not reduce diversity by suppressing the growth of less competitive sown forbs. In fact, none of the subordinate sown forb species were affected by spatial structure at all. Lower diversity in the uniformly sown treatment compared to our monospecifically aggregated treatment was caused by the disproportionate benefit experienced by aggressive sown species. In highly aggregated restorations, abundances of fast growing species are limited by spatially restricted resources and intra-specific interactions. As aggregation decreased and fast growing species are more widely distributed, traits that confer high fitness may allow them to capitalize on greater amounts of spatially available resources and increase in abundance. Conservative sown prairie species such as *A. canescens*, (lower fitness) may not have as great of a positive response to decreasing aggregation at this early stage in community development because they may be more limited by inherent slow growth rates than by spatially limited resources.

Because of the slow growth rates among many of the sown species in our communities, the effects of initial spatial arrangement may be primarily experienced between weeds and dominant sown species. The inverse relationship between $C_4$ grass and weed abundance is consistent with patterns predicted under spatial competition theory. In our communities, when superior competitors (*R. pinnata, S. nutans, P. virgatum*) and inferior competitors (weeds) are universally distributed within a community (UNIFORM treatment), weeds are excluded relatively quickly. This is consistent with previous studies that show the suppressive effect of $C_4$ grasses on weed establishment (Wilsey 2010, Török et al. 2010). However, when dominant natives are aggregated into patches (AGMON, AGRAN, and AGRED), spatial refuges are created for weeds where they can persist, which is consistent with the prediction made in spatial coexistence theory.

Porensky et al. (2012), looked at the effects of experimentally aggregated and interspersed grassland communities, and found that aggressive species have higher abundances in interspersed communities compared to aggregated ones as in our study. In interspersed communities (similar to our uniform communities) aggressive species were able grow rapidly and fill much of the available space. In aggregated communities, aggressive species were not able to colonize much of the community area, preventing them from becoming very abundant across the entire community. Similarly, Stoll and Prati (2001) found that the growth of competitively superior species is restricted when they are spatially aggregated in plant communities.

To determine how interactions among sown species of multiple functional groups affect coexistence, some experimental treatments included restorations with functionally similar or dissimilar patches of species. Chessen's coexistence framework predicts that if the stabilizing effects of niche differences are relatively strong, communities where functionally dissimilar species are aggregated (AGCOM) should exhibit greater diversity and inferior competitors should persist. Alternatively, if fitness differences between functionally different species overwhelm the effects of niche differences, communities where functionally similar communities are aggregated (AGRED) should exhibit greater diversity and inferior competitors should persist. We found no difference in relative sown species composition, diversity, or evenness between restorations with functionally similar or functionally dissimilar patches. The only difference we found was greater sown grass abundance in the AGCOM treatment compared to the AGRED treatment which likely reflects the effects of less aggregated spatial structure more than the effects of interaction among functional groups. The lack of effects in diversity and composition suggests that differences in species' fitness and functional niches don't substantially affect the strength of plant-plant interactions of the native sown species at this early in restoration. The AGCOM had lower weed cover than AGRED treatment. This is, on the surface, consistent with the niche-based hypothesis that complementary species mixtures will result in reduced invasion by weeds – presumably because complementary mixtures would more fully utilize resources than redundant mixtures. However, it is more likely that patches within complementary restorations contain species from the grass and tall forb groups that effectively suppress weed species. Our initial predictions regarding differences in diversity and composition between the AGRED and AGCOM treatments based on spatial coexistence theory were based on the assumption that the strongest interactions would occur primarily among sown species. However, because the abundances of many sown species are very low at this early stage of community development, such effects may not have emerged yet.

While the abundance of two dominant grass species and three tall forb species all increased with decreasing aggregation, the cause may differ among species. The absolute abundances of *R. pinnata, S. nutans*, and *S. scoparium* in monospecifically aggregated patches are very high, suggesting that these species may be limited by density dependent self-limitation due to intra-specific competition. A lower level of aggregation likely relieves this self-limitation and allows them to become more abundant. The two less aggressive forb species (*Heliopsis helianthoides* and *Monarda fistulosa)* that differ in abundance among our treatments also have higher abundances in less aggregated communities where they interact with large, competitive species. In fact, their abundances are relatively low in monospecifically aggregated communities where there is very little inter-specific competition and highest in uniformly sown communities where inter-specific competition is highest. There are multiple reasons for this. This trend could result from Janzen-Connell type dynamics (for review, see Comita et al. 2014) where, in less aggregated communities, species are released from density-dependent limitation resulting from specialized natural-enemies. While this may influence the abundance of sown species, it is likely a minor influence. If the negative effects of host specific pathogens are strongly enhanced by spatial aggregation, we would expect to see lower abundance of aggregated species in other studies. But other studies have found that less competitive species perform better when aggregated (Stoll and Prati 2001, Porenski et al. 2012, Yurkonis & McKenna 2014).

It is more likely that the higher abundance of *H. helianthoides* and *M. fistulosa* in uniformly sown communities is due to direct or indirect facilitation by the most abundant prairie species. The early establishment of fast growing sown species could facilitate the growth of subordinate sown species by creating favorable growing conditions at the soil surface or by releasing subordinate species from suppression by weeds (indirect facilitation). The lack of dominant sown species such as *S. nutans* and *R. pinnata* in the monospecific patches of these two species may allow weeds to establish and suppress their growth (Figure 1.7). One important feature of our study is that we did not actively remove weeds from our restorations. Other studies, which have found that subordinate species benefit from aggregation, have minimized the role of weeds by either limiting weed establishment in the field (Stoll and Prati 2001, Porenski et al. 2012) or conducted studies in pots where weeds were not an issue (Yurkonis & McKenna 2014). The high abundance of weed species facilitated by spatially restricted competitive sown species may suppress some slow-growing forb species (Blumenthal et al 2003). This result, which deviates from the results of other studies, show that implementing spatial structure in tallgrass prairie restorations may lead to different outcomes compared to those seen under more controlled settings (and outcomes predicted by theory) because of intense interaction between sown species and weeds.

While the higher total sown abundance in uniformly sown communities generally supports the use of uniform sowing strategies to establish prairies, this may be a transient state made possible by the relatively low amount of grass seed used in our study (25%) compared to other restorations (80%). This low grass seed density may only delay the potential suppression of forbs by $C_4$ grasses observed in other studies (McCain et al. 2010, Packard and Mutel 1997, Weber 1999, Kindscher and Fraser 2000, Dickson and Busby 2009). Later in succession, $C_4$ grasses may become more abundant and exclude forb species decreasing the diversity of our uniformly structured communities (Sluis 2002, Camill et al. 2004) and in complimentary aggregated communities. In aggregated communities, if the suppressive effects of $C_4$ grasses are limited by restricted spatial distributions and forb species become more abundant, aggregated restorations may result in highly desirable communities. Peter Schramm initiated restorations in the 1960's using aggregated spatial structure similar to our treatments. Vegetation surveys showed that, within Schramm's "mosaic" restorations, slow growing species may require more than five years to become established (Sperry 1983). However, spatially aggregated restorations have higher mean conservatism values and a similar floristic quality index (FQI) than nearby remnants many years after restoration (Allison 2002). Whether or not our restorations approach or diverge from predictions of coexistence theory will be addressed by ongoing surveys.

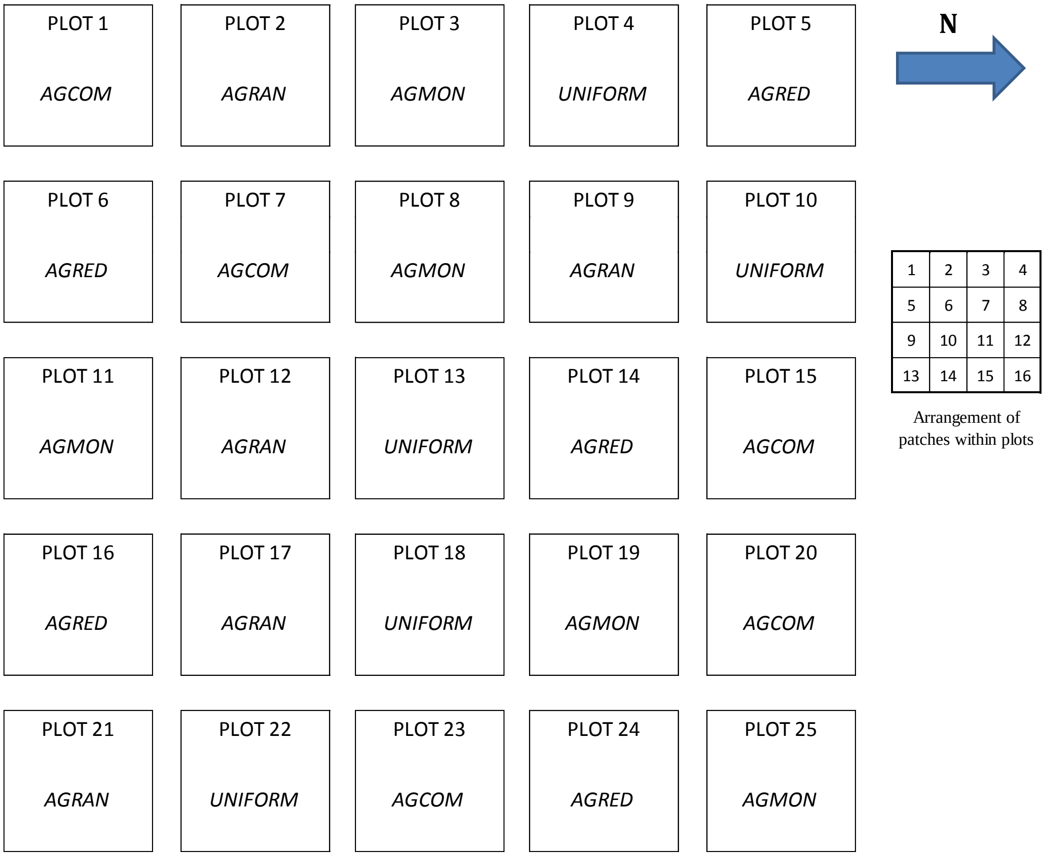
While we cannot provide a specific prescription for implementing spatial structure into restorations based on our initial results, we have learned that the effects of spatial aggregation are complicated by the presence of weeds. Because of this, practitioners should be cautious about implementing spatial planting methods based on results from controlled studies. While it may be appealing to completely exclude grasses from patches within restorations to promote the growth of forbs, grasses are effective at suppressing weed species and completely excluding them could result in high weed abundances and lower forb abundance requiring additional time and money to remedy. Early in succession, highly aggregated plant communities have higher weed abundance and lower forb cover observed with no apparent advantage. However, spatially isolating particularly aggressive species could offer some benefit. Some practitioners have identified the aggressive nature of some grasses and forbs and have completely excluded them from restorations to increase the abundance and diversity of forb species with reasonable success However, we argue that these species are important and should be included in restorations. Aggressive species such as *S. nutans* and *R. pinnata* can be included in restorations while minimizing their potential to outcompete subordinate species by sowing them in “islands” in a restoration instead of including them in homogenized seed mixes.

Our study advances the current understanding of how spatial structure regulates plant community coexistence in the early stages of restoration. Our results suggest that as species are beginning to establish, spatial structure shifts the composition of plant communities by dictating the outcomes of interaction among fast growing, dominant species. The effects of spatial structure on less abundant species may take longer to realize.

## Tables and figures

Table 1.1: Plant species experimentally sown with their family, metabolic pathway, range of height at maturity, and their functional group designation used to determine species sown in patches within the AGCOM, AGRAN, and AGRED aggregation treatments. Taxonomy follow USDA plant database (https//:plants.usda.gov)

| Species | Six letter speceis code | Family | Metabolic pathway | Plant height (m) | Functional group designation |
|---|---|---|---|---|---|
| Andropogon gerardii | Andger | Poaceae | $C_4$ | 1.3-2.0 | $C_4$ grass |
| Schizachyrium scoparium | Schsco | Poaceae | $C_4$ | 0.6-1.3 | $C_4$ grass |
| Panicum virgatum | Panvir | Poaceae | $C_4$ | 1.0-2.0 | $C_4$ grass |
| Sorgastrum Nutans | Sornut | Poaceae | $C_4$ | 1.0-1.6 | $C_4$ grass |
| Amorpha canescens | Amocan | Fabaceae | $C_3$ | 0.6-1.0 | Legume |
| Dalea purpurea | Dalpur | Fabaceae | $C_3$ | 0.3-1.0 | Legume |
| Desmanthus illinoensis | Desill | Fabaceae | $C_3$ | 0.6-1.0 | Legume |
| Lespedeza capitata | Lescap | Fabaceae | $C_3$ | 0.6-1.3 | Legume |
| Coreopsis lanceolata | Corlan | Asteraceae | $C_3$ | 0.3-0.6 | Short Forb |
| Echinacea pallida | Echpal | Asteraceae | $C_3$ | 0.6-1.0 | Short Forb |
| Coreopsis palmata | Corpal | Asteraceae | $C_3$ | 1.0-2.0 | Short Forb |
| Penstemon digitalis | Pendig | Scrophulariaceae | $C_3$ | 1.0-1.6 | Short Forb |
| Ratibida pinnata | Ratpin | Asteraceae | $C_3$ | 1.0-1.6 | Tall Forb |
| Monarda fistulosa | Monfis | Lamiaceae | $C_3$ | 0.6-1.3 | Tall Forb |
| Heliopsis helianthoides | Helhel | Asteraceae | $C_3$ | 1.0-2.0 | Tall Forb |
| Helianthus maximiliani | Helmax | Asteraceae | $C_3$ | 1.0-3.0 | Tall Forb |



| | | | | |
|---|---|---|---|---|
| PLOT 1<br>*AGCOM* | PLOT 2<br>*AGRAN* | PLOT 3<br>*AGMON* | PLOT 4<br>*UNIFORM* | PLOT 5<br>*AGRED* |
| PLOT 6<br>*AGRED* | PLOT 7<br>*AGCOM* | PLOT 8<br>*AGMON* | PLOT 9<br>*AGRAN* | PLOT 10<br>*UNIFORM* |
| PLOT 11<br>*AGMON* | PLOT 12<br>*AGRAN* | PLOT 13<br>*UNIFORM* | PLOT 14<br>*AGRED* | PLOT 15<br>*AGCOM* |
| PLOT 16<br>*AGRED* | PLOT 17<br>*AGRAN* | PLOT 18<br>*UNIFORM* | PLOT 19<br>*AGMON* | PLOT 20<br>*AGCOM* |
| PLOT 21<br>*AGRAN* | PLOT 22<br>*UNIFORM* | PLOT 23<br>*AGCOM* | PLOT 24<br>*AGRED* | PLOT 25<br>*AGMON* |

| | | | |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| 5 | 6 | 7 | 8 |
| 9 | 10 | 11 | 12 |
| 13 | 14 | 15 | 16 |

Arrangement of patches within plots

Figure 1.1: The layout of plots (and patches within them) at the field site and their treatment designations. 25 10 x 10m plots consist of 16, 2.5 x 2.5m patches each. Plots are separated by with AGMON=monospecifically aggregated, AGRED = species with that are functionally similar, or redundant, were sown in the same patch, AGRAN = random subset of four species were sown into each patch, AGCOM = functionally dissimilar, or complementary, species were sown into each patch, UNIFORM = all species were sown uniformly in all patches

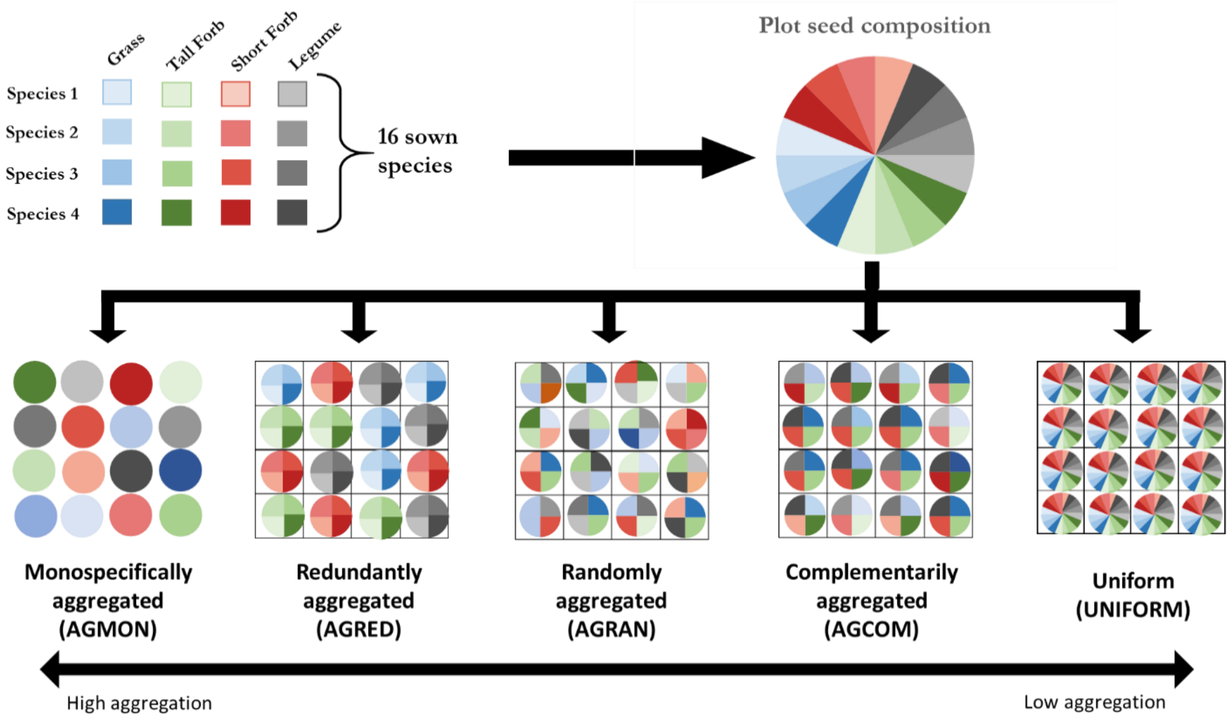


Figure 1.2: Each of the 16 species seeded are represented by a unique color. Species within a functional group are represented with unique shades of the same base color (top left). The composition of each plot (individual grid) represents an experimental restoration where the community composition are identical with each species equally represented (large pie chart), and only differ in the spatial arrangement of the 16 species. The five plots in the figure represent one block of the experiment. Each plot is subdivided into 16 patches (small grid squares), which serve as individual units of aggregation for each treatment. The species specified by the small pie charts within each patch indicates the species that are sown within each patch. The size of the wedge is equal to the proportion of seed present for each species. Figure 3: The layout of plots (and patches within them) at the field site and their treatment designations. 25 10 x 10m plots consist of 16, 2.5 x 2.5m patches each. Plots are separated by with AGMON=monospecifically aggregated, AGRED = species with that are functionally similar, or redundant, were sown in the same patch, AGRAN = random subset of four species were sown into each patch, AGCOM = functionally dissimilar, or complementary, species were sown into each patch, UNIFORM = all species were sown uniformly in all patches.

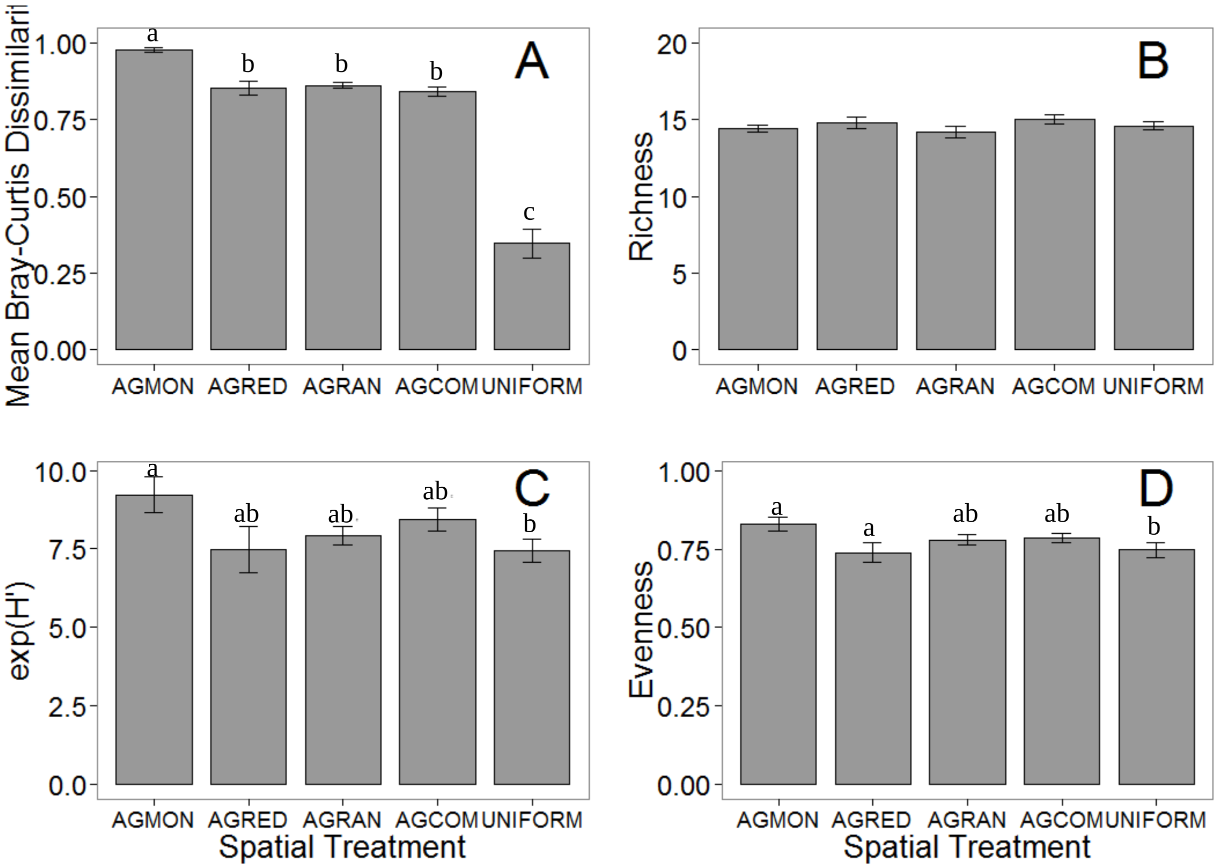


Figure 1.3: **A:** Mean Bray-Curtis dissimilarity of patches within plots of each treatment with **B:** Mean richness of plots of each treatment. **C:** Mean exponential of Shannon diversity of each treatment. **D:** Mean evenness of each treatment. Error bars indicate standard errors (+/- 1SE). Letters indicate significant differences among groups tested with Tukey pairwise tests.

Table 1.3: Results of ANOVA I testing native community attributes (Mean ± 1 SE)

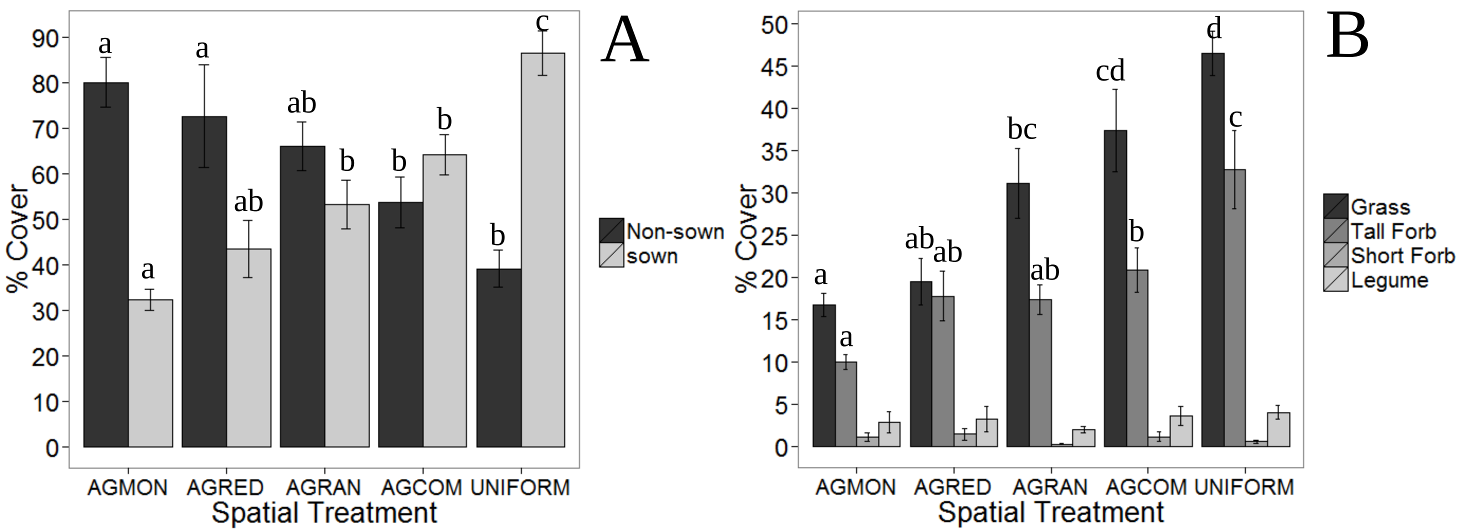


Figure 1.4: **A.** Mean absolute % cover (+/- 1 SE) of total sown and total non-sown cover of each spatial aggregation treatment. **B.** The mean absolute % cover of the four functional groups sown within each spatial aggregation treatment. Plant groups indicated in the legend from top to bottom are grouped in the figure from left to right. Letters indicate significant differences among treatments within the same functional group tested with Tukey pairwise tests.

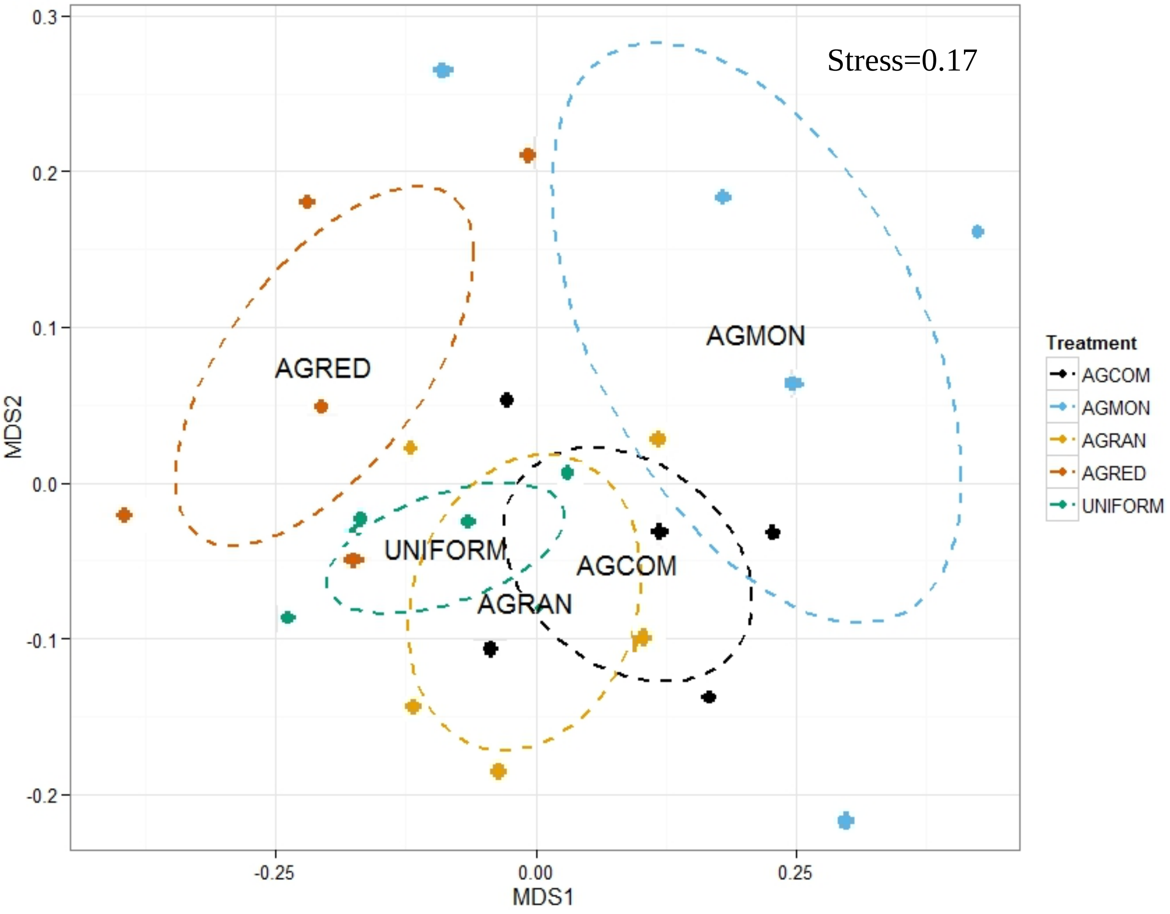


Figure 1.5: NMDS ordination showing relative sown species composition. Each point represents one experimental plot. Ellipsoids indicate the 95% confidence interval for the centroid of each treatment.

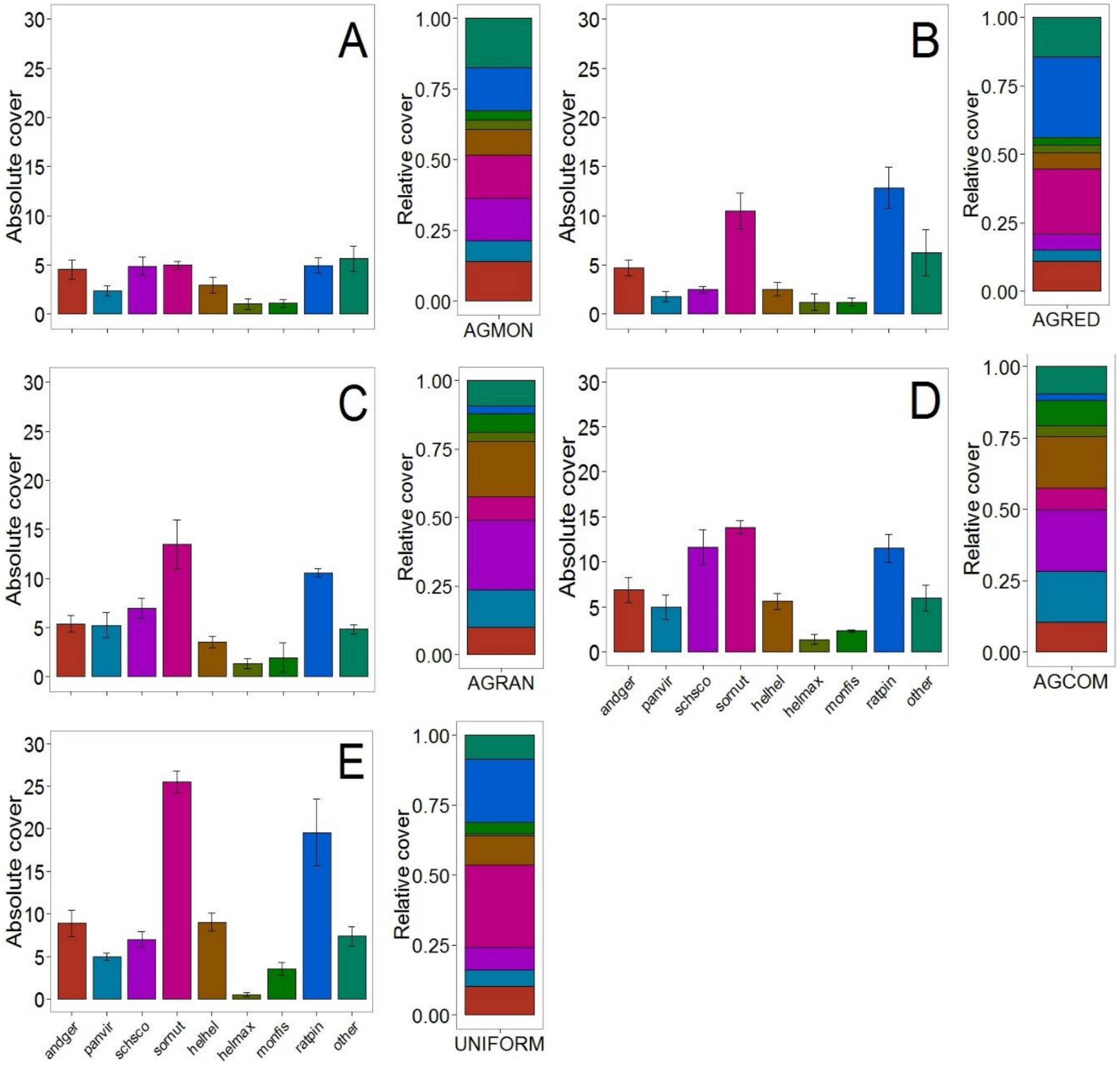


Figure 1.6: The relative and absolute abundances (mean +/- SE) of species within the tall forb and grass functional groups (groups that showed significant difference in absolute abundance) in all spatial treatments. The "other" category indicates the sum of absolute and relative cover values in the respective figures of the sown species within the short forb and legume functional group categories. **A.** Absolute (left) and relative (right) abundance of sown species within the AGMON treatment. **B.** Absolute and relative abundances of sown species within the AGRED treatment. **C.** Absolute and relative abundances of sown species within the UNIFORM treatment. **D.** Absolute and relative abundances of sown species within the AGCOM treatment. **E.** Absolute and relative abundances of sown species within the AGRAN treatment. The legend refers to each species by the first three letters of the genus and first three letters of the species name (example: *Andropogon gerardii* = "andger"; see Table 1 for full Latin and common names). The same colors are used to represent species in the figures showing the absolute cover values and the relative cover values.

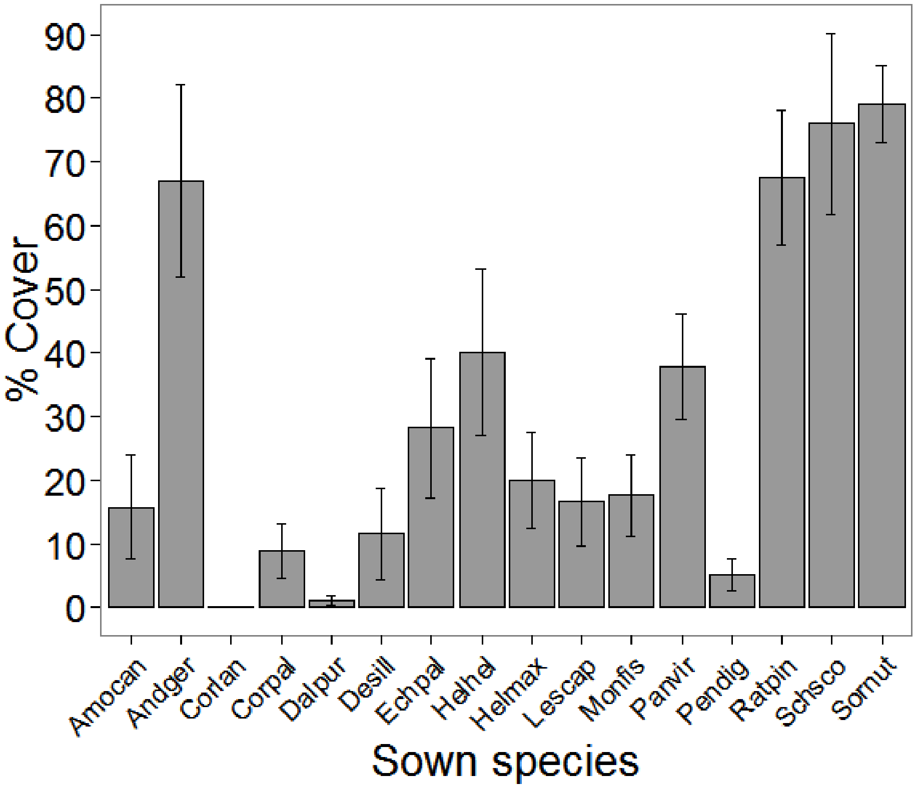


Figure 1.7: Absolute cover (mean +/- SE) of all sown species in monospecific patches of the AGMON treatment plots. Species abbreviations refer to the first three letter of the genus and species names (example: *Andropogon gerardii* = "Andger"; see Table 1 for full Latin and common names).

# Chapter 2

## Are native tallgrass prairies more resistant to invasion than abandoned cropland? A landscape-scale study of *Lespedeza cuneata*

## Abstract

Invasive plants are a widespread economic and ecological burden to society. Invasive species research has focused on understanding how propagule pressure, disturbance, and the invasion resistance of the plant community influence their spread. However, at large scales these factors are often confounded with one another making it difficult to determine if there differences in the intrinsic invasion resistance between plant communities and understand the relative importance of these factors. Here, we study the role of these factors by focusing on the large-scale invasion of one exotic invasive plant species that is problematic in Midwestern grasslands: *Lespedeza cuneata* (Sericea). The goals of this study are to 1) to determine if there are intrinsic differences in the invasion resistance of grassland types to Sericea: abandoned cropland and native tallgrass prairie, 2) to understand how variation in propagule pressure and disturbance across the landscape influences Sericea invasion, and 3) understand the relative contributions of these factors. We did this by comparing observed patterns of Sericea invasion at Fort Riley Military Reserve (FRMR) to null models of invasion. We also tested whether or not there is a spatial association between Sericea invasion and military activity, distance to seed source, and grassland type using the PCNM spatial modeling approach in combination with variance partitioning analysis. We found that tallgrass prairie is intrinsically more resistant to Sericea invasion than abandoned cropland, but this invasion resistance can be overwhelmed by high levels of military activity. Military activity appears to promote Sericea invasion, in part, by aiding the dispersal of seeds. We also found that more modest degradation to native communities can lead to reductions in invasion resistance. Our results offer insights to the importance of propagule pressure, community invisibility, and disturbance at large scales and reveal factors contributing the landscape-scale invasion of Sericea.

## Introduction

Invasive plants are a widespread economic and ecological burden to society (Pimental et al. 2005). To limit any future spread and impacts, research has focused on understanding how disturbance, propagule pressure, and the properties of the recipient community influence their establishment and spread. However, understanding the relative importance of these factors at large spatial scales is difficult. While some small scale experimental studies have been able to demonstrate the contributions of these factors (Naeem et al. 2000, Wardle 2001, Holle and Simberloff 2005, Belote et al. 2008, Eschtruth and Battles 2009), it is not clear how they influence invasion at large scales because they are often spatially confounded. Plant communities thought to be intrinsically less resistant to invasion (such as species poor or highly disturbed communities) may show higher levels of invasion than other such communities simply because they experience higher levels of propagule pressure (Williamson 1996, Lonsdale 1999, Colautti et al. 2006). Here, we attempt to overcome this common limitation by using spatial modeling approaches with variance partitioning analysis as well as null modeling approaches to examine how potential differences in the invasion resistance, disturbance, and propagule pressure affect the distribution of *Lespedeza cuneata* (Dum. Cours. G. Don; Sericea) across a heterogeneous landscape in Eastern Kansas.

Sericea is an herbaceous legume native to Southeast Asia that was introduce into the U.S. in 1896 (Ohlenbusch and Bidwell 2001). Sericea was promoted for erosion control, wildlife habitat, and livestock forage by conservation departments (Pieters 1950) and was used to stabilize soil following road construction which expedited its dispersal around the Midwest. Sericea populations that originally established from these practices have spread into pasture lands where it decreases the economic value of grazing land (Fechter and Jones 2001) and into native grasslands where it decreases native plant cover and richness (Brandon et al. 2004). In an effort to control Sericea, some states have passed legislation to prevent its distribution (NRCS 2016) and land managers use herbicide to control established populations (Missouri Department of Conservation 2016). While these control efforts are necessary, the amount of land invaded by Sericea continues to grow (Kansas Department of Agriculture 2013).

Sericea invasion may be facilitated by the widespread occurrence of agricultural land that may be more susceptible to invasion. Studies have shown that disturbed areas often have greater exotic invasion than their natural counterparts (Lundgren et al. 2004, Von Holle and Motzkin 2007, Brown and Boutin 2009). It is thought that natural communities may have higher invasion resistance than disturbed ones, in part, because natural communities effectively reduce resources needed for invaders to establish. (Elton 1958, Tilman 1996). This reduction in resources may be driven by higher plant diversity, which has been shown to increase invasion resistance (Tilman 1997, Naeem 2000, Kennedy et al. 2002) or by the presence of a few competitive plant species that efficiently utilize resources (Grime 1998, Crawley et al. 1999, Lepš et al. 2001, Wardle 2001, Smith et al. 2004). In the Midwest, agriculture has altered the vast majority of grasslands from diverse, native vegetation toward a degraded and functionally different composition consisting of exotic, cool-season grass species. Exotic, cool season grass species often utilize soil resources less efficiently than native warm-season species (Tilman and Wedin 1991) leaving soil resources available for invaders to potentially utilize (Tilman 1996, Davis et al. 2000, Shea and Chesson 2002). However, it is often difficult to determine if differences in the structure or composition of plant community correspond to differences in invasion resistance because disturbed areas often experience higher levels of propagule pressure than relatively natural sites. This makes it difficult to distinguish to what degree these two potential factors contribute to invasion success (Williamson 1996, Lonsdale 1999, Hierro et al. 2005).

It is well known that propagule pressure substantially influences invasion success (Brown and Peet 2003, Rouget and Richardson 2003, Foxcroft et al. 2004), So to understand if there are intrinsic differences in invasion resistance among plant community types, it is necessary to account for propagule pressure in large-scale studies (Rouget and Richardson 2003). This can be difficult because human activities that contribute to the dispersal of invasive propagules may occur disproportionately in disturbed areas (Lonsdale 1999, McKinney 2002, Taylor and Irwin 2004). Both intentional and unintentional human-aided dispersal has contributed to Sericea's regional distribution (Hoveland et al. 1971). At the landscape scale, humans may contribute to Sericea's spread by unintentionally dispersing seeds by vehicles and on clothing. Both of these dispersal vectors have been demonstrated with other species (Clifford 1959, Wichmann et al. 2009 ,Veldman and Putz 2010) and can facilitate the spread of invasive species (Von der Lippe and Kowarik 2007). If Sericea seeds area dispersed by human activity, the number of propagules transported to an area may also be affected by the distance to the nearest Sericea population.

Aside from differences in invasion resistance of grassland types and propagule pressure, Sericea invasion may be associated with unidentified abiotic or biotic, autocorrelated features of the landscape. If there is no attempt made to control for the effects of unmeasured autocorrelated variables in observational studies, the effects of propagule pressure, disturbance, and grassland type may be confounded. Fortunately, advances in spatial statistics allow us to potentially identify spatial patterns in a response variable apart from those of the explanatory variables;

isolating the effects of explanatory variable from potentially influential, but unmeasured autocorrelated features of the landscape.

In this study I explore the potential importance of propagule pressure, disturbance, and land-use/habitat type in affecting the spatial distribution of Sericea invasion in a large multi-use landscape. Fort Riley Military Reserve (FRMR), in Northeastern Kansas, provides a unique opportunity to study how these factors contribute to Sericea invasion across a large and varied landscape. Due to the very shallow soil in the Flint Hills eco-region, much of the land within the base has never been cultivated and is still dominated by native prairie species, while some fertile areas were previously farmed. This has resulted in a patchwork of two distinct grassland types: remnant tallgrass prairie and abandoned cropland (Figure 2.1a). From 2003 to 2012, Sericea has aggressively spread throughout FRMR. However, but it did not spread uniformly. Proportionately, abandoned cropland has experience more Sericea invasion than tallgrass prairie at Fort Riley (Figure 2.1b and c, Figure 2.2a and b) consistent with the theory that diverse native communities are more resistant to invasion than disturbed ones.

The primary objective of this study is to determine to what degree this pattern of invasion reflects differences in the intrinsic invasion resistance of the two grassland types (prairie versus abandoned cropland) or differences in propagule pressure and disturbance. FRMR provides a unique opportunity to study the influence of these potentially confounding factors because the location, frequency, and type of ongoing military activity (a major source of disturbance) are well documented. Because the locations of Sericea populations and different grassland communities are well documented, we are also able to partially account for differences in propagule pressure throughout FRMR by calculating the distance of each area from the nearest seed source (established Sericea populations). Utilizing military training records from 2007-2012 collected by FRMR, vegetation surveys in 2002 and 2011, and invasive species surveys collected at FRMR from 2008-2011, we address the following questions:

1) What are the relative contributions of grassland type, military activity, and seed source distance to the distribution of Sericea invasion?
2) To what extent is the observed lower invasion of tallgrass prairie a result of higher invasion resistance, versus lower propagule pressure? Also, are tallgrass prairies that have been moderately degraded less resistant to invasion than those that are relatively less degraded?
3) Is the spread of Sericea influenced by dispersal limitation? If so, does military activity facilitate Sericea invasion by overcoming such limitations?

If Sericea invasion is facilitated by military activity, the spatial distribution of military activity at FRMR will be similar to Sericea's distribution. In this case, the density of Sericea plants will increase as the intensity of military activity increases. However, an association between military activity and Sericea invasion does not distinguish between the potential confounded effects of dispersal and disturbance caused by military activity. Sericea invasion may be facilitated by military activity primarily through its effects on seed dispersal or through its disturbance to the plant community. If military activity does not promote Sericea invasion, military activity will not influence the distribution or density of Sericea. If native tallgrass prairie communities are more resistant to invasion than abandoned cropland, abandoned cropland should have higher rates of invasion after controlling for propagule pressure and military activity. If tallgrass prairie and abandoned cropland are equally susceptible to Sericea invasion, then invasion rates into each grassland type should reflect the area each grassland type occupies in the landscape. If disturbance increases the susceptibility of tallgrass prairie to Sericea, native prairies with relatively degraded plant communities will experience higher rates of invasion than those relatively intact.

## Methods

### *Study site*

Our study area is the 101, 600 acre Ft. Riley Military Reservation (FRMR) located in Geary and Riley counties, Kansas in the Flint Hills tallgrass prairie eco-region (Figure 2.1a). Because the Flint Hills have very shallow soils and are often unsuitable for farming, large tracts tallgrass prairie remain at FRMR. In fertile areas of the base, there are large contiguous tracts of land that were once used for cropland, but are now abandoned. Abandoned cropland contains few native tallgrass species and are dominated by exotic grass species. Tallgrass prairies at FRMR have not been cultivated and are dominated by native tallgrass prairie species. Variation in land-use history across the site has resulted in a patchwork of large tracts of two different grassland types: remnant tallgrass prairie and abandoned cropland (Figure 2.1a). Both grassland types are currently used for military training activities and both experience variable levels of disturbance because military exercises are not conducted uniformly across the base. Because permanent training facilities and roads have been built at specific sites within FRMR, areas close to those permanent facilities are used for troop exercises and heavy machinery maneuvers frequently while much of the reserve is used for training infrequently (Figure 2.1d). Activities are conducted in defined areas of FRMR referred to as “training areas” (Figure 2.3). Sericea has been spreading across FRMR over the last two decades and now covers a large percentage of the base (Figure 2.1c).

### *Vegetation surveys*

We used two sets of vegetation surveys for our analyses. The first was a set of surveys conducted by The Kansas Biological Survey (KBS) in 2002-2003 and in 2011-2012 that mapped the location and condition of vegetation at FRMR, including the location of Sericea. In each FRMR training area, surveys: 1) Located areas dominated by grassland communities previously used for crop production and those dominated by native tallgrass species and designated them as "abandoned cropland" and "flint hills tallgrass prairie" respectively; 2) Located populations of Sericea; and 3) assessed the overall quality of tallgrass prairies. Crews of one or two people on foot or using ATVs attempted to visually cover the entirety of each training area. No attempt was made to conduct vegetation surveys using more refined methods such as transects or quadrats due to the large amount of land surveyed (Freeman and Delisle 2004). In these surveys, the fundamental units of sampling were the training areas (Figure 2.3). The locations of Sericea plants were recorded using hand-held Garmin GPS units. If a large, dense Sericea population was found, the perimeter of the population was designation with GPS points. Point data was exported into ArcGIS to delineate the boundaries of Sericea populations. Sericea population boundaries were also drawn on aerial photographs and entered into ArcGIS using head's up digitizing. Any two plants closer than 100 m were mapped as part of the same occurrence to avoid mapping dozens of small occurrences. Dead Sericea plants were excluded from estimates (Freeman and Delisle 2004). KBS's surveys produced maps of the locations of each grassland type and the spatial distribution of Sericea presence and absence across the entire base (Figure 2.1a, b, c). The land area occupied by each grassland type and the area occupied by Sericea within each training area (Sericea's spatial distribution) was used as the predictor and response variables in our PCNM analysis.

We also used prairie quality assessments conducted during the KBS surveys to determine if there were differences in the invasion resistance among prairies that differ in their overall condition. Prairie quality assessments were done for tallgrass prairies greater than 10 acres. The quality of prairies was determined by assessing the landscape condition around each prairie, the size of the prairie, and the vegetation condition of native species within each prairie. The landscape condition of each prairie was given a grade from A-D. The primary factor determining the grade of the landscape condition was the percent of surrounding area considered natural. Prairies with less natural area surrounding them received lower grades. Each prairie was also given a grade from A-D based on the size of the prairie assessed by vegetation maps. Smaller prairies received lower grades. Finally, the vegetation condition of each prairie was given a grade from A-D based on the floristic quality index (FQI) of native species present in the prairie. The presence or abundance of invasive species (including Sericea) was not used to assess the quality of prairies. The grade of the three individual components were then combined to produce a single quality grade for each prairie at FRMR. For a more thorough explanation of the grading system, see Delisle et al. (2012). Generally, higher grade prairies were larger, tended to have more conservative plant species, and existed in more natural landscapes compared to lower grade prairies.

To analyze how military activity affects the density of Sericea plants within each training area, we used a second set of Sericea surveys conducted by staff at FRMR. Because KBS surveys used point data to identify general areas that Sericea occupied, they could only be used to analyze broad patterns in Sericea's distribution (PCNM analysis) and could not be used to assess differences in Sericea plant density.  FRMR surveys were performed from 2008-2011. Because of the widespread invasion of Sericea at the FRMR, only portions of the base could be surveyed and treated each year so the surveys conducted by FRMR do not include all training areas. FRMR staff walked or drove straight line transects roughly 100 m apart over the entirety of each training area and recorded the spatial location of Sericea populations using handheld GPS units. For each point, an estimate of the plant density of the immediate area was specified. Unlike surveys done by KBS, all locations of Sericea populations were recorded using GPS points true to their spatial location. Because the KBS surveys were intended to produce population distributions, some populations were recorded by generating GPS points along the perimeter of Sericea populations preventing accurate estimates of plant density.

### *Military Activity*

To determine how military activity affected the distribution of Sericea, some measure of the intensity of military activity and its spatial location was needed. To estimate the relative intensity of military activity across the base, we combined vehicle and troop training records collected by FRMR with vehicle track densities estimated from satellite images. When military training was scheduled at FRMR, the type and number of vehicles used for a training activity as well as the number of troops trained were recorded for each training area at FRMR. We added together the number of vehicles used and added together the number of troops trained in each training area from 2007-2012 and relativized both sets of values. The relativized vehicle values were multiplied by two, then added to the relativized troop values. Multiplying the relativized vehicle values by two was done to give more mathematical weight to the vehicle values because exercises conducted with heavy machinery likely cause more disturbance than those conducted without them. Staff at FRMR indicated that while military exercises could have utilized the entire training areas, vehicle maneuvers were consistently carried out in areas close to permanent facilities. To capture the variation in intensity within training areas, we quantified the density of heavily used vehicles tracks across the base by digitizing vehicle tracks visible in satellite images using ArcGIS. Finally, we added the combined relativized values to the track density values in ArcGIS to produce a single variable that quantifies the intensity of military activity across the base (Figure 2.1d).

Since we had no direct measure of propagule pressure or seed dispersal across FRMR, we used distance from the nearest Sericea population as a surrogate for propagule pressure. Distance to nearest Sericea population was calculated by first dividing the area of FRMR into many 1m$^2$ units, then we calculated the distance from each unit to the nearest Sericea population identified in 2003 KBS surveys (Figure 2.1b) using ArcGIS. This resulted in a spatially continuous distribution of distances across FRMR that provided some estimate of the relative amount of propagule pressure across the base.

### *Data analysis*

Abandoned cropland and tallgrass prairie occupied the vast majority of land at FRMR (Figure 2.2a and b). There were numerous other plant community types at FRMR, but they covered such little area that even after combining them into one category (“other”), they were a very minor component of the landscape (Figure 2.2). Because tallgrass prairie and abandoned cropland comprised the majority of land within FRMR, we focused our analyses on these two grassland types.

One goal of this study was to determine the relative importance of disturbance, grassland type, and propagule pressure in the distribution of Sericea invasion. To do this, we used variance partitioning analysis to separate the individual contributions of military activity, grassland type, and distance from nearest Sericea population from the effects of the spatial relationship among sampling sites. For our sampling units, we used the training areas defined by FRMR because these areas were the smallest units in which records of military activity were kept. Training areas were similar in size. For each training area, we calculated the percent area occupied by Sericea (response variable) by dividing the total area occupied by all Sericea populations by the total area of each training area. We also calculated the percent area occupied by both grassland types (two different predictor variables) using the same strategy. Since mean military use intensity and the mean seed source distance (also predictor variables) were spatially continuous variables, we calculated the weighted mean of both in ArcGIS for each training area. This calculated the mean of a continuous variable by weighing each value of the variable of interest by the proportion of area each value occupied. This produced one mean value of military use intensity and seed source distance for each training area. We collectively refer to the four predictor variables listed above as “landscape” variables.

To disentangle the potential differences in inherent resistance from propagule pressure, military activity, and disturbance, we used variance partitioning analysis to estimate their independent and combined effects. In the variance partitioning analysis, we controlled for potentially influential, but unmeasured variables by including a set of spatial predictor variables created using principle component of neighbor matrices (PCNM; Borcard and Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). This method first created a truncated distance matrices derived from latitude and longitude values associated with the sample locations (training areas). This modified distance matrix was then subjected to principal coordinates analysis (PCoA) that resulted in orthogonal eigenvectors that were used as spatial predictor variables. We refer to the aggregate of these eigenvector predictor variables as “spatial” predictor variables. This modelling approach can detect spatial structures in response data. When included in our variance partitioning analysis these spatial predictor variables quantified the proportion of the variation in

Sericea's distribution due to the landscape variables independent of their spatial structure (Figure 2.4; fractions that do not contain "d"), the proportion of variance explained by the joint effects of spatial structure and our landscape variables (Figure 2.4; fractions containing "d" and other variables), and the proportion explained by the spatial structure of sites independent of landscape variables (Figure 2.4; independent "d" fraction). We used the "PCNM" package in R version 3.2.1 to create these spatial variables. From the total set of spatial eigenvectors generated by PCNM, we only used eigenvectors with positive eigenvalues because we were only interested in spatial structures present in Sericea's distribution with positive spatial autocorrelation. Our response variable for this analysis was the proportion of each training area invaded by Sericea. The landscape and spatial predictors were independently regressed on our response variable to determine which subset of the spatial and landscape variables significantly affected Sericea invasion. In the regression model testing the environmental variables, we applied a log+1 transformation on the response variable and to the environmental variables to meet the assumptions of linear regression. In the regression model testing the spatial variables, a log+1 transformation was only applied to the response variable. The predictor variables in the spatial regression model were forward selected with the Blanchet et al. (2008) double stopping criterion before variation partitioning. The spatial variables retained in the model were then used for variance partitioning. We did not forward select variables included in the regression model testing landscape variable, but used the variables that were significant in the variance partitioning analysis. Redundancy analyses and permutational tests were performed on each unique fraction of the variance partitioning analysis to test their significance (Legendre et al. 2011, Legendre and Legendre 2012).

Another goal of this study was to determine if tallgrass prairie is more resistant to Sericea invasion than abandoned cropland. Results from the variance partitioning procedure above allowed us to evaluate the importance of grassland type relative to other factors, but does not demonstrate differences in invasion resistance between tallgrass prairie and abandoned cropland. It also does not demonstrate if changes in the overall condition of native communities affects their invasion resistance. Lastly, it does not show how potential differences in invasion resistance among these communities are affected by military activity and by proximity to seed sources. To understand these relationships, we conducted three sets of comparisons between the observed patterns of Sericea invasion and null models of Sericea invasion. The null models simulated Sericea invasion by redistributing the invaded area equally among grassland types proportional to the area they occupy in the landscape, while holding military-use intensity and distance from seed source constant. This allowed us to determine if the observed levels of invasion in each grassland type deviated from what is expected under the null expectation (equally invaded) in the absence of other factors.

The first set of comparisons was done to determine if there were differences in the intrinsic invasion resistance of tallgrass prairie and abandoned cropland. Here, it was necessary to control for the potentially confounding effects of military activity that may have encouraged invasion. We created a randomization procedure in Python programming language (version 2.7.11) that simulated Sericea invasion into tallgrass prairie and abandoned cropland by redistributing the invaded area between the two grassland types within discrete bins of military-use activity. Military-use intensity (a spatially continuous variable) was binned into arbitrary categories of equal intervals. Because there were few areas at FRMR with very high military use intensity, we combined multiple bins with very high values so that the total land areas in each of the new larger bins was sufficient to minimize very large stochastic variation. Once the values of military use intensity within each bin were defined, we identified the geographic areas of FRMR that fell within each category of military use intensity and calculated the area of abandoned cropland, the area of tallgrass prairie, and the area of each grassland type invaded using ArcGIS. For each bin of military use intensity, the total invaded area was divided into 100 m x 100 m (1 hectare) units which were then redistributed between the two grassland types such that the probability that a given unit of Sericea is distributed to each grassland type was equal to proportion of land they occupied. The unit size was chosen because the surveys used to establish the size of Sericea populations counted individual plants within 100 m of each other as the same population. Because the proportion of abandoned cropland and tallgrass prairie were different in each military use bin, the odds that a given unit of Sericea was distributed into either of the grassland types was also different for each military use category. After the invaded area is redistributed, the area of abandoned cropland and tallgrass prairie "invaded" in our simulation was calculated. This randomization was repeated 100 times for each bin. We calculated the mean of the 100 runs for invaded abandoned cropland and invaded tallgrass prairie. Ninety-five percent confidence intervals were calculated for the simulated invasion means by ordering the simulated values from low to high and identifying the simulated values that corresponded to the fifth and ninety-fifth percentile of the list of simulated values.

The second set of comparisons was performed similarly to the first. In this comparison, invaded area was redistributed among tallgrass prairies that varied in their overall condition. For each bin of military used, the areas occupied by A, B, C, and D quality prairies were calculated along with the total invaded area (as described above). Then, the invaded area was redistributed among all prairies proportional to the area they occupied in the landscape. In this model, the total area invaded by Sericea was calculated only for tallgrass prairies that were assessed for their overall quality, which excluded all other plant community types.

A third set of comparisons was done to determine if Sericea invasion was affected by dispersal limitation and how military activities may affect dispersal limitation. We examined how the likelihood of sites becoming invaded was influenced by their proximity to established Sericea populations in areas with high and low military-use intensity. To do this, we first identified areas that surrounded Sericea populations present at FRMR in the 2003 vegetation surveys (Figure 2.1b) in 100m increment “bands” up to 1000m using ArcGIS. Then, similarly to the methods used for previous analyses, we calculated the area within each 100m band occupied by tallgrass prairie, abandoned cropland, and Sericea. Unlike the previous two sets of comparisons, areas of each of the grassland types and for Sericea were only calculated within two military-use intensity categories. These two bins were chosen because they were the highest and lowest bins of military-use intensity represented in all distances bands (100m-1000m). Analyzing the effects of proximity to seed sources in areas with little military activity and high military activity allowed us to determine if Sericea invasion was affected by dispersal limitation and how military activity affected such limitations. To estimate the area invaded by Sericea within each military use bin if there were no dispersal limitation, we totaled the invaded area of all distance bands together and then redistributed the invaded area among all distance classes based on the proportion of land they occupied in each military use bin in one hectare units. This was done for tallgrass prairie and abandoned cropland.

The modeling procedures used above were able to determine if the area invaded in each grassland type deviated from what is expected if both were equally resistant to invasion. However, this analysis did not indicate if the severity of invasion increases with increased human activity. To determine this, we performed a simple linear regression with mean military-use intensity of each training area (described above) as the predictor and density of Sericea in each training area as the response. For this regression, we used Sericea surveys conducted by FRMR staff. In these surveys, each of the GPS points created to locate Sericea plants were categorized as “low” density (1-10 plants), “moderate” density (10-20 plants), or “high” density (20-30 plants). To quantify the density of Sericea plants, we counted the number of GPS points in each category and multiplied each category by the mean number of plant for that category (low = 5, moderate = 15, high = 25). Then we added those values together to estimate the number of plants encountered in each training area. We divided this estimate by the area of each training area to control for variations in training areas’ size. If training areas were surveyed in more than one year, we used the most recent year’s survey for our estimates. Only 55 of the 101 training areas at FRMR had been surveyed for Sericea from 2008-2011. Those that were not surveyed were not included in the analysis. We performed a log+1 transformation on the predictor and response variables to meet the assumptions of linear regression.

## Results

When the invaded area of each grassland type was calculated, the majority of Sericea invasion occurred in tallgrass prairie and cropland (Figure 2.2a). While tallgrass prairie occupied a slightly higher absolute area at FRMR, the percent of tallgrass prairie invaded (25%) was much lower than the percent of abandoned cropland invaded (64%), and the “other” community types had little invasion (Figure 2.2b).

### *PCNM analysis*

Military use intensity, proportion of abandoned cropland, and mean seed source distance were retained as significant predictors of Sericea invasion in our multiple linear regression, but proportion of tallgrass prairie was not (Table 2.1). Sericea invasion was positively related to military use intensity and proportion of abandoned cropland but was negatively related to seed source distance. The total model explains 68% of the variation in Sericea invasion among training areas (before considering the effects of space via PCNM variables). In a separate forward selection procedure conducted on the PCNM variables, thirteen of the original thirty-eight eigenvectors with positive eigenvalues were retained (Table 2.1). The overall model was highly significant.

Variance partitioning reveals that the spatial predictor variables, military activity, seed source distance and grassland type together explained 75.2 % of the variation in Sericea distribution across FRMR. Spatial predictor variables in aggregate, grassland type, and seed source distance explained significant portions of Sericea's distribution independent of the other variables, but military activity did not (Figure 2.4). Spatial variables, either uniquely or in combination with grassland type, seed source distance, or military activity explained 60.2% of the variation in Sericea invasion (Figure 2.4, portions containing "d"). Of this, 11.4 % is explained by the joint effects of grassland type and the spatial variables, 2.3 % is explained by the joint effects of military activity and spatial variables, and 11.3% is explained by seed source distance and spatial variables. The joint effects of all variables (Figure 2.4, center-"a-b-c-d") explained 14.1 % of the variation in Sericea's distribution and 10.8 % is explained by the spatial variables independent of the landscape variables. Only 6.8% of the total variation is explained by landscape variables independent of the spatial variables (Figure 2.4, portions that do not contain "d") and 20.8% of the variation is not explained by the variables included in our models.

*Sericea density regression*

We performed a linear regression to determine if military activity affects the severity of Sericea invasion as measured by the density of Sericea plants across FRMR. Our regression showed a significant and positive relationship between the two ($\beta$=0.65, $t_{1, 55}$=3.33, $P$<0.01, adj$R^2$=0.15). As the intensity of military activity increased among training areas, the density of Sericea individuals also increased. The intercept was also significantly different from zero ($\beta$=0.94, $t_{1, 55}$= 5.731, P<0.001).

*Invasion model comparisons*

The observed levels of Sericea invasion in tallgrass prairie and abandoned cropland deviated from levels that would occur if both grassland types were equally resistant to invasion (Figure 2.5). While we did not perform a statistical test to establish differences between observed and simulated invasion, the observed invasion falls far outside of the confidence interval for the simulated invasions in most military use categories. In areas where the intensity of military use is relatively low, our comparisons showed that the null expectation was for tallgrass prairie to have more invaded area than abandoned cropland, but the observed pattern of invasion was the opposite. In fact, for most categories of military-use intensity, abandoned cropland had more area invaded than was expected and tallgrass prairie had less. The magnitude of these differences was greatest at very low military-use intensity and decreased as intensity increased. At very high levels of military use intensity, differences between the simulated and observed populations diminished.

To determine if the invasion resistance of tallgrass prairie communities was dependent on their overall condition (a single categorical variable derived from the landscape condition around each prairie, the size of the prairie, and the FQI of native species within each prairie), we simulated Sericea invasion into tallgrass prairies by redistributing the invaded area equally among all native prairies regardless of their overall condition. This simulation showed that the observed invaded area deviated from what was expected if prairies were equally resistant to invasion. The observed level of invasion in grade A prairies (those that are least degraded and surrounded with natural areas) below the 95% confidence intervals of our simulated invasion in all but three military-use categories (Figure 2.6a). This was not true for military-use categories two, seven, and eight. Grade B prairies showed a similar pattern as grade A prairies where the observed invaded area fell below the confidence interval of the simulated invasion for five of the eight military-use categories. However, the absolute difference between the simulated and observed invasions appeared to be less than in grade A prairies (Figure 2.6b). Military-use categories two, four, and eight fell within the confidence intervals. In grade C prairies, differences between observed and simulated invasion were much smaller. While the observed areas of invasion fell below the margin of error of the simulated invasion in five of eight military-use categories, the absolute difference between them was very small (Figure 2.6c). The observed level of invasion was within the margin of error in categories two, three, and six. In grade D prairies, the observed invasion fell above the margin of error of the simulated invasion (Figure 2.6d). The only instance where this was not true was in the highest level of military- use intensity. The absolute difference between the observed and simulated invasion was the largest of any of the prairie invasion comparisons.

To determine if dispersal limitation affected Sericea invasion and how high military use may affect dispersal limitation, we simulated Sericea invasion along a distance gradient from established Sericea populations. The simulated invasions provided an estimate of how much area would have been invaded in each distance band if all distances were equally likely to be invaded. Put more simply, the simulated invasions were null models that estimated Sericea invasion assuming no dispersal limitation. We compared observed and simulated levels of invasion in abandoned cropland and tallgrass prairie in areas of high and low military use intensity. In areas of low military use intensity, simulated levels of invasion deviated from observed levels of invasion in abandoned cropland and prairie (Figure 2.7 c and d). In both grassland types, the observed level of invasion at sites relatively close to established populations were higher than the simulated levels and at relatively far distances, the observed invasion was lower than simulated levels. In areas with high military use, there was very little difference between the observed and simulated levels of invasion (Figure 2.7 a and b). In abandoned cropland, observed invasion levels fell within the margin of error of simulated levels in every distance band. In tallgrass prairie, the observed levels fell outside of the margin of error in only the 100m, 200m, and 500m distance bands.

## Discussion

The goals of this study are: 1) to determine the relative contributions of grassland type, military activity, and seed source distance to the distribution of Sericea invasion. 2) Determine to what extent the observed lower invasion of tallgrass prairie a result of higher invasion resistance, versus lower propagule pressure. We also investigated whether moderately degraded prairies are less resistant to invasion than those that are relatively less degraded. 3) Determine if the spread of Sericea is influenced by dispersal limitation and how military activity may facilitate Sericea invasion by overcoming such limitations.

To do this, we performed a simple linear regression to determine if there is a relationship between military-use intensity and the density of Sericea plants across FRMR. We also quantified the relative importance of military activity, and grassland type by using PCNM and variance partitioning analyses. We compared observed levels of Sericea invasion to a series of null models that assumed invasion rates were equal among all sites to specifically identify how grassland type, military activity, and propagule pressure combine to affected invasion. We also wanted to determine if patterns of invasion deviated from expected invasion patterns if these factors had no effect.

In our variance partitioning analysis, the 12.9% of the variation explained by grassland type alone and the portion jointly explained by spatial variables and grassland type are consistent with the hypothesis that tallgrass prairie communities are inherently more resistant to Sericea invasion than abandoned cropland. This analysis controls for the effects of military activity and distance to seed source that also influence the large-scale distribution of Sericea. The variation jointly explained by spatial and landscape variables indicates the degree to which the spatial structures of landscape variables induce a similar spatial structure in the response variable (Sericea distribution). The substantial amount of variation explained by grassland type and spatial variables suggests that Sericea invasion is dependent on the distribution of the two grassland types. The portion of variation explained by grassland type alone represents relationships between Sericea and grassland type associated with local conditions (biotic or abiotic characteristics of the community) apart from the effects of the x-y coordinates of sampling locations. This may indicate that there are populations of Sericea at FRMR that occur in abandoned cropland that cannot be explained by identified spatial patterns. It is possible a rare dispersal event could have transported Sericea seeds to only a few locations, allowing Sericea to establish populations that are spatial outliers.

Our simulations, which finely tested differences in the invasion rates between grassland types, showed that after controlling for the potentially confounding effects of seed dispersal and disturbance from military activity, tallgrass prairie is more resistant to Sericea invasion than abandoned cropland. This result is consistent with invasion theories that relate the invasion resistance of communities to resource availability such as the diversity-invasibility theory (Elton 1958), fluctuating resources (Davis et al. 2000), and the dominance of competitive species (Grime 1998, Crawley et al. 1999) among many others. It is also consistent with studies that have found invasive species over-represented specifically in old-field systems (Lundgren et al. 2004, Domènech et al. 2005) and with those that show invasive species are more common in highly man-made and historically disturbed areas (Lonsdale 1999, Hobbs 2000). Our results are also consistent with Foster et al. (2015) that conducted experimental Sericea invasions into tallgrass prairie and abandoned cropland. In their study, propagule pressure was controlled experimentally and they found that tallgrass prairie is more resistant to Sericea invasion than abandoned cropland at high and low levels of propagule pressure. However, our results deviate from theirs in that the enhanced invasion resistance of tallgrass prairie can be overwhelmed by high levels of disturbance and propagule pressure caused by human activity. As military activity reached very high levels at FRMR, the proportion of land invaded by Sericea increased until it reached approximately 100%; the same as abandoned cropland.

There are several reasons why abandoned cropland may be less resistant to invasion than tallgrass prairie. Abandoned cropland has likely experienced chronic disturbance from tillage, vehicle traffic, etc. that could have a direct effect on invasion resistance. Lower diversity often seen in abandoned cropland may also affect invasion resistance. Experimental evidence suggests that plant communities with higher diversity are less susceptible to invasion (for review, see Levine and D’Antonio 1999) possibly because of more complete resource utilization by functionally complementary plant species (Tilman 1996). Some of the invasion resistance observed in prairies may be attributable to the abundance of particular competitive species.

Multiple studies have shown that the identity of dominant species can significantly affect invasion resistance (Crawly et al. 1999, Tracy and Sanderson 2004, Emery and Gross 2007). It is possible that that dominant $C_4$ grasses in tallgrass prairie are better competitors for limiting resources in grassland communities making it more difficult for invasive species to establish. $C_4$ grasses utilize nitrogen and water more efficiently than cool-season grasses (Tilman and Wedin 1991) that dominate abandoned cropland. $C_4$ grasses also experience most of their growth in the warm months of the year similar to Sericea, whereas cool-season grasses grow vigorously in the spring and fall.

Invasion resistance of the two grassland types is drastically affected by the intensity of military activity. Our variance partitioning analysis shows that the distribution of military activity influences the distribution of Sericea at FRMR and areas used most intensely are much more likely to be invaded by Sericea. Additionally, results from our simulations show that, in areas with very high levels of military-use, differences in invasion resistance between tallgrass prairie and abandoned cropland completely diminish and 100% of both grassland types were invaded. This suggests that intrinsic differences in invasion resistance between the two grassland types can be overwhelmed by the effects of disturbance.

The influential role of military activity at FRMR on Sericea invasion is not unique to our study. Our results are consistent with the general association between human activity and exotic species invasion (Lonsdale 1999, Meyerson and Mooney 2007, Richardson and Pysek 2006). At FRMR, the individual effects of propagule pressure and disturbance due to military activity are completely confounded. The dispersal of weed seed by vehicles is common (Clifford 1959, Rew and Flemming 2011, Taylor et al. 2012) and can be a significant vector for seed dispersal (Ansong and Pickering 2013, Veldman and Putz 2010). Our comparisons between observed invasion and null models of invasion support dispersal of Sericea by military vehicles. When we compared observed and simulated levels of Sericea invasion in areas with little military activity, there were higher rates of invasion near established Sericea populations than would be expected if there was no effect of distance. Areas far from Sericea populations experienced lower rates of invasion than expected. This suggests that in the absence of human activities, Sericea experiences dispersal limitation. In areas with high military activity, sites of all distances are invaded at the same rate suggesting that human activities are dispersing Sericea beyond what it is capable of naturally. Once seeds arrive in new locations, the disturbances caused by tank and Humvee traffic may promote Sericea establishment by changing soil texture, increasing bare ground, lowering soil carbon, and increasing soil compaction (Althoff et al. 2010). Furthermore, the disturbance from military vehicles can degrade native communities (Althoff et al. 2009, Howard et al. 2013, Retta et al. 2013) that may be more easily tolerated by Sericea compared to native vegetation.

Military activity not only affects Sericea's distribution, but also the density of Sericea plants. We found that as the areas of FRMR are used more extensively, the density of Sericea plants increases. A photograph taken at FRMR (Figure 2.8) shows an area of tallgrass prairie where Sericea had densely established in the tracks left by military tanks, but was much less established around the tracks where native vegetation is intact. This photo provides some additional evidence that military activity promotes Sericea invasion.

Native communities that are in relatively poor condition, likely cause by moderate past disturbances, have lower invasion resistance. In our comparisons between the observed and simulated invasion, high quality and low quality prairies are not equally resistant to invasion. Over a range of military use intensity, higher quality prairies are more resistant to invasion than low quality prairies. Lower quality prairies may have experienced some type of moderate disturbance in the past not captured in our data, which reduced their invasion resistance. Vegetation surveys did not assess the composition and diversity of prairie so we are unable to associate differences in invasion resistance with characteristics of the community. One possibility is that the natural areas surrounding higher quality prairies act as buffers that resist invasion better than the disturbed areas surrounding lower quality prairies. From other analyses, we know that abandoned cropland is less resistant to invasion and may act as corridors that increase the number of propagules entering low qualities prairies.

The portion of variation explained by spatial variables independently of military activity and grassland type in our variance partitioning analysis could be due to unmeasured and spatially structured environmental variables. Such variables could include natural soil conditions, species interactions, or topography that influence which sites become invaded by Sericea. It is possible that efforts to control Sericea with herbicide by FRMR staff are influencing its spatial distribution as well. Staff at FRMR indicated that herbicide treatments are routinely done in a subset of the training areas each year. Large, contiguous tracts are often selected for treatment to avoid conflicting with training activities. Herbicide is applied with aerial sprayer or large equipment to maximize the area treated.

The results of this study help clarify the role of invasion resistance in plant invasion into natural and disturbed plant communities. Most attempts to isolate the effects of invasion resistance in plant communities have been done with small, controlled invasions into synthetic communities (Knops et al. 1999; Naeem et al. 2000; Hector et al. 2001, Foster et al. 2015). Results from studies that examined the interaction between disturbance, propagule pressure, and invasion resistance have seen mixed results. Some show that propagule pressure overrides other factors to drive invasion success (Holle and Simberloff 2005, Eschtruth and Battles 2009), while others have found that biotic features of the community can stave off invasion- even at relatively high propagule pressure (Byun et al. 2015, Foster et al 2015). One shortcoming of large-scale studies that examine differences in invasion rates between disturbed and natural areas is that they often do not control for propagule pressure and disturbance, which are known to influence invasion (Levine and D'Antonio 1999; Shea and Chesson 2002). This is likely because they are very difficult to quantify over large scales. Here we have shown, that after controlling for these confounding factors, native tallgrass prairie is more resistant than abandoned cropland to invasion at large scales. This brings to light an important ecosystem service provided by native tallgrass prairie, which have been almost completely removed from the landscape and gives additional justification for their restoration. More work should be done to investigate the potential use of tallgrass prairie restoration as a means to resist Sericea invasion or exotic invasion in general.

## Tables and Figures

Table 2.1: Results of the multiple regression analyses of military-use, seed source distance, grassland type and spatial predictor variables included in the variance partitioning analysis with percent of each training area occupied by Sericea as the response variable. The reduced model after forward selection of the spatial variables is shown as most spatial variables in the model were not significant.

| | t | *p* | β | cum *adj.* $R^2$ | *F* | *df* | adj. $R^2$ |
|---|---|---|---|---|---|---|---|
| Military activity and Land-use (whole model) | | | | | | | |
| Overall Model | | <0.001 | | | 55 | 6 | 0.68 |
| (intercept) | -0.4 | 0.63 | 3.51 | | | | |
| military activity | 5.1 | <0.001 | 0.59 | | | | |
| abandoned cropland area ( | 6.9 | <0.001 | 0.39 | | | | |
| prairie land area (%) | -0.1 | 0.86 | 0.13 | | | | |
| seed source distance | -7.1 | <0.001 | -0.54 | | | | |
| Spatial variables (forward selected) | | | | | | | |
| Overall Model | | <0.001 | | | 7.7 | 38, 60 | 0.72 |
| PCNM 2 | | 0.001 | | 0.26 | 37.1 | | |
| PCNM 8 | | 0.001 | | 0.34 | 11.4 | | |
| PCNM 5 | | 0.003 | | 0.40 | 12 | | |
| PCNM 13 | | 0.002 | | 0.47 | 12.8 | | |
| PCNM 1 | | 0.002 | | 0.52 | 12 | | |
| PCNM 15 | | 0.001 | | 0.57 | 10.9 | | |
| PCNM 4 | | 0.004 | | 0.61 | 10.3 | | |
| PCNM 18 | | 0.01 | | 0.63 | 7.3 | | |
| PCNM 10 | | 0.005 | | 0.66 | 7.5 | | |
| PCNM 3 | | 0.015 | | 0.68 | 6.7 | | |
| PCNM 12 | | 0.027 | | 0.69 | 4.8 | | |
| PCNM 29 | | 0.035 | | 0.70 | 4.5 | | |
| PCNM 19 | | 0.042 | | 0.72 | 4.5 | | |

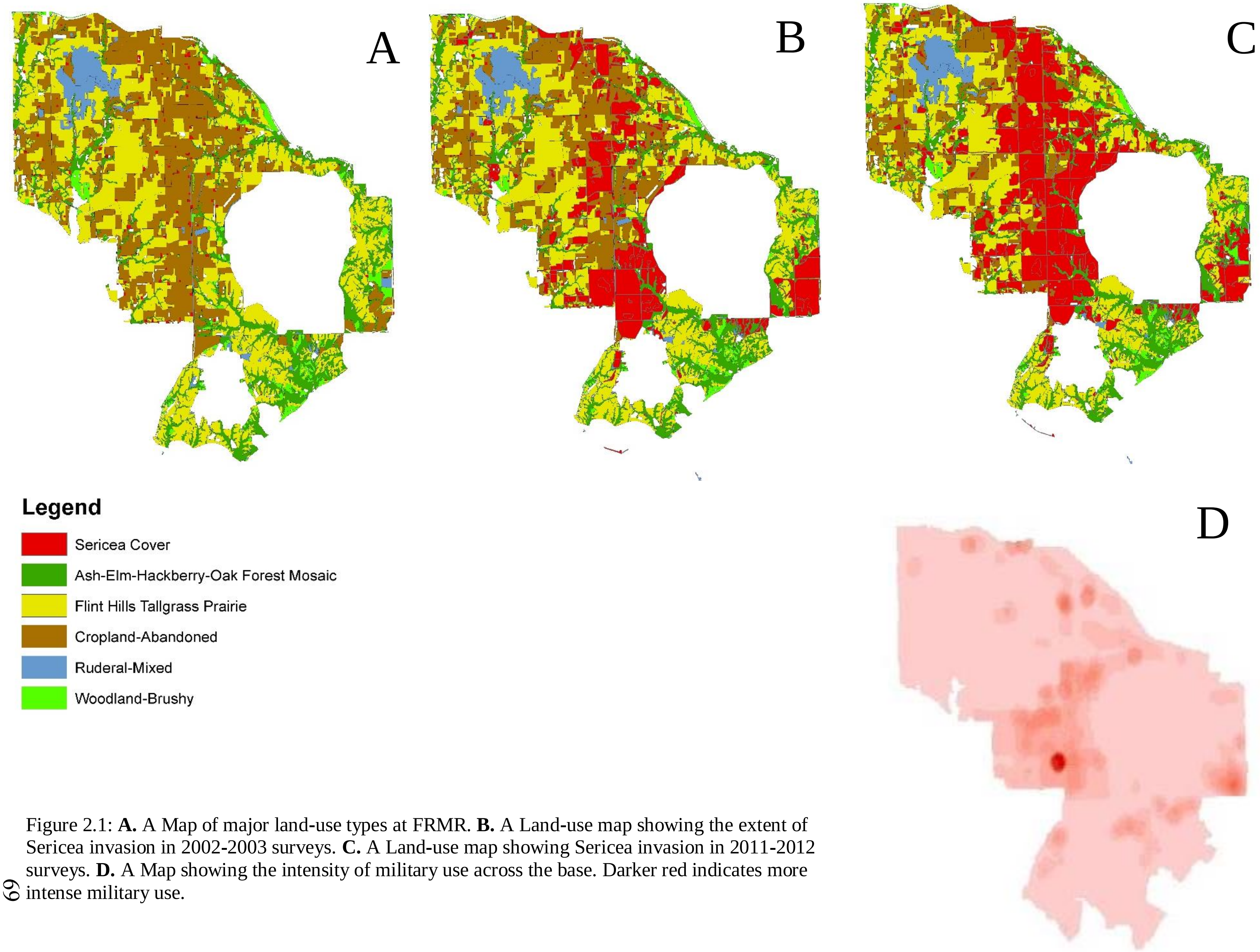


Figure 2.1: **A.** A Map of major land-use types at FRMR. **B.** A Land-use map showing the extent of Sericea invasion in 2002-2003 surveys. **C.** A Land-use map showing Sericea invasion in 2011-2012 surveys. **D.** A Map showing the intensity of military use across the base. Darker red indicates more intense military use.

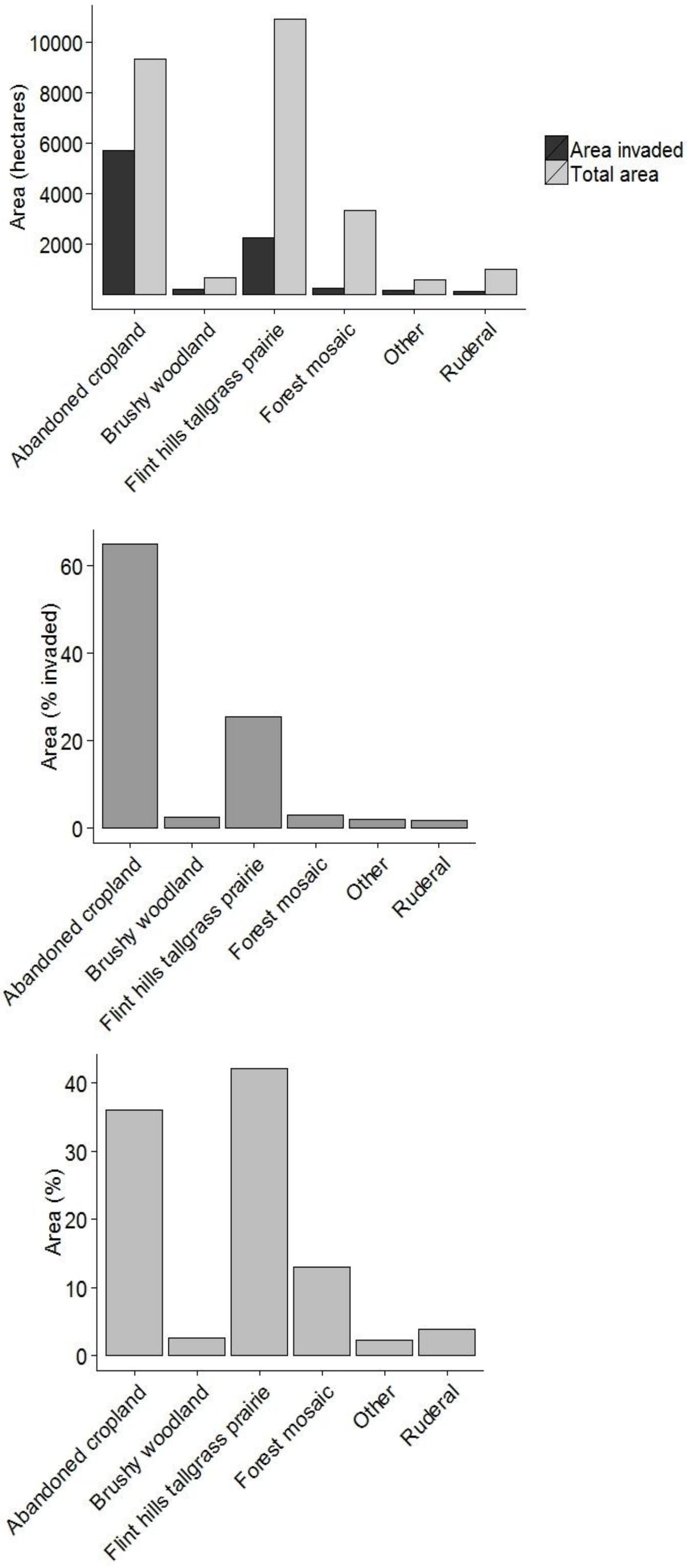


Figure 2.2: **A.** The absolute area of land of each plant community type occupied at FRMR and the absolute area invaded by Sericea. **B.** The percent of each plant community type invaded at FRMR. **C.** The percent of total area at FRMR that each plant community type occupies.

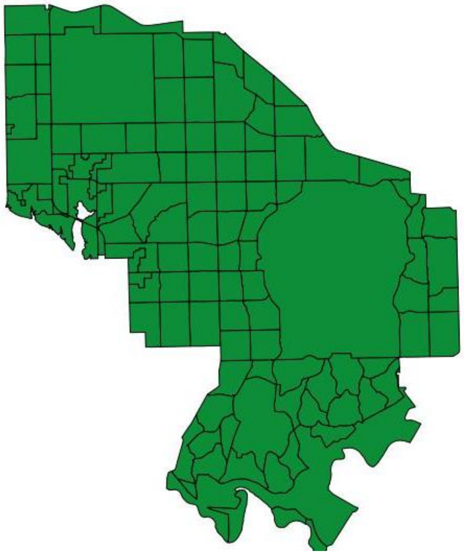


Figure 2.3: A map of the 101 training areas at FRMR. The large area toward the right is the “impact area” where artillery training is conducted. The large square area near the upper left contains additional facilities and is not a training area.

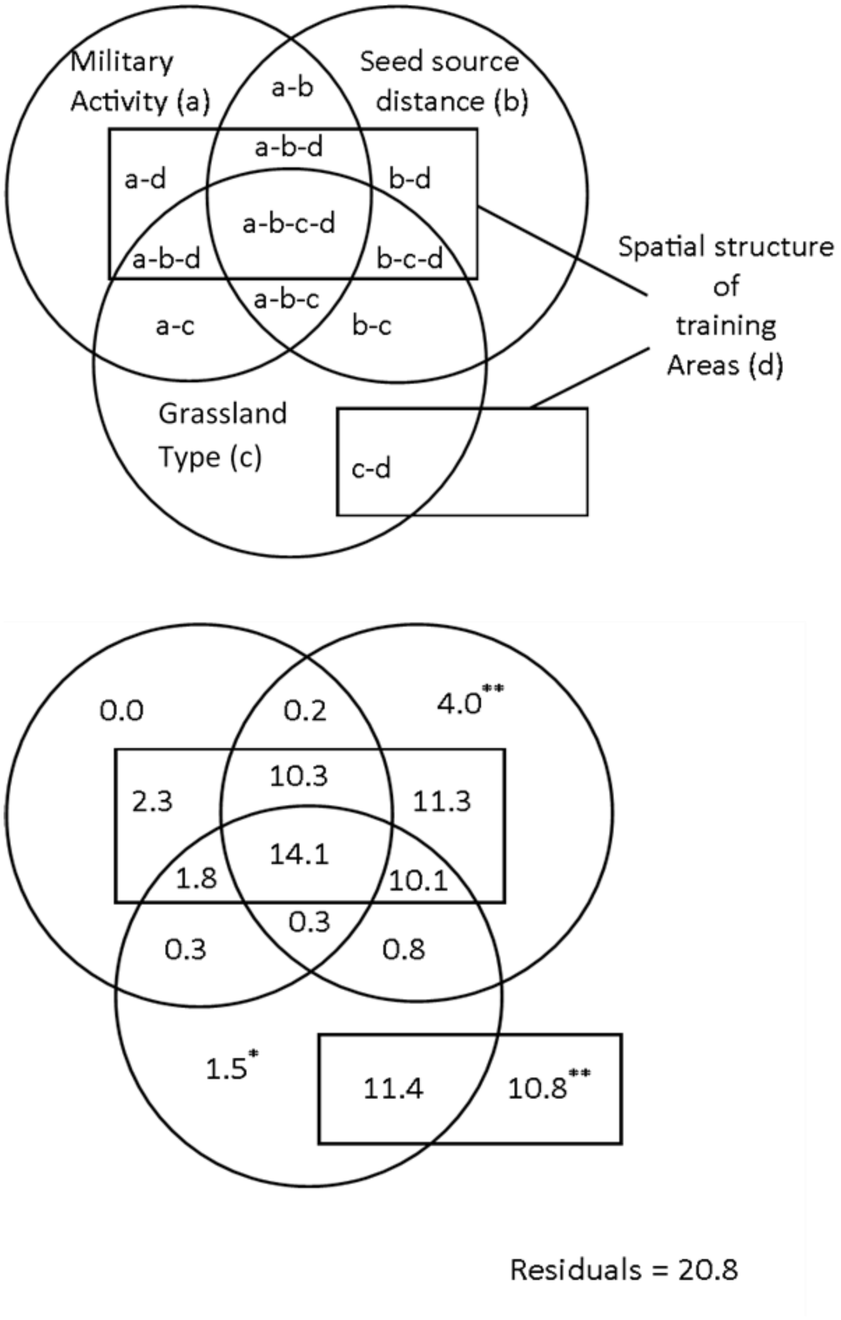


Figure 2.4: Venn diagram showing the percentage of variation in Sericea into training areas due to military use intensity (a), seed source distance (b), percentage abandoned cropland (c), and spatial variables (d) and combinations thereof.. Letter combinations in each overlapping area reflect the percentage of variation explained by the joint effects of those variables (e.g. a-b is joint effects of Military use intensity and seed source distance). Only the proportions of variation contributed by each factor independent of the others were tested. * P<0.05, ** P<0.01.

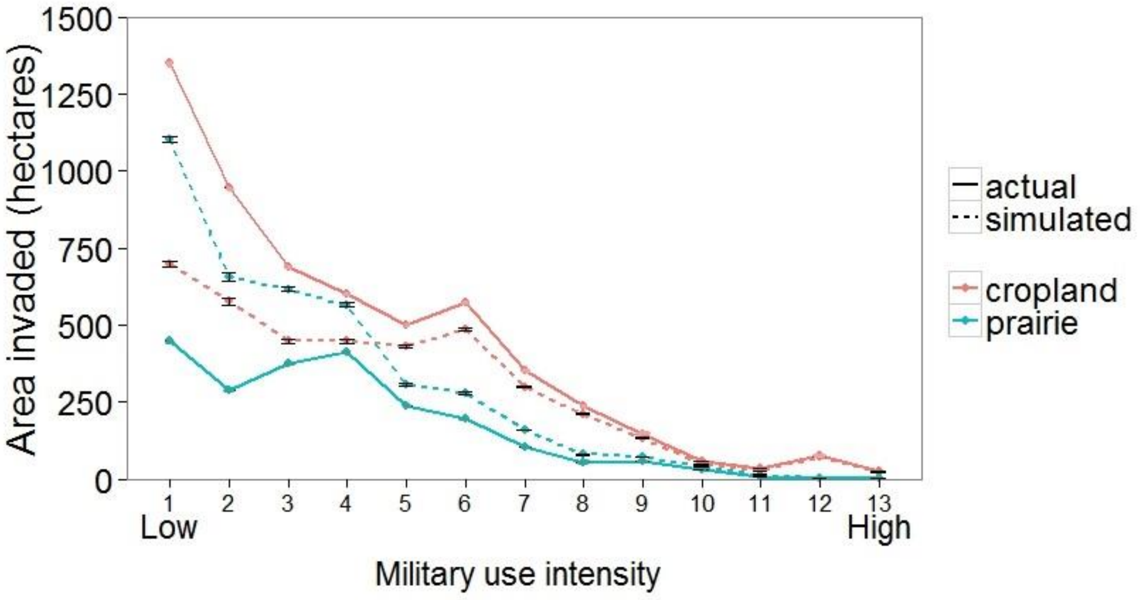


Figure 2.5: Shows the observed and simulated area invaded by Sericea in abandoned cropland and in tallgrass prairie. The number on the x axis are arbitrary, but represent a gradient of military use intensity from low to high calculated at FRMR. Error bars show 95% CI for 100 simulations. Note that this does not show the cumulative invaded area, but the area invaded for each category of military use intensity. The lines decrease rapidly from left to right because the total land area which experience low levels of use is very large, but the amount of land that experience very high intensity use is very small.

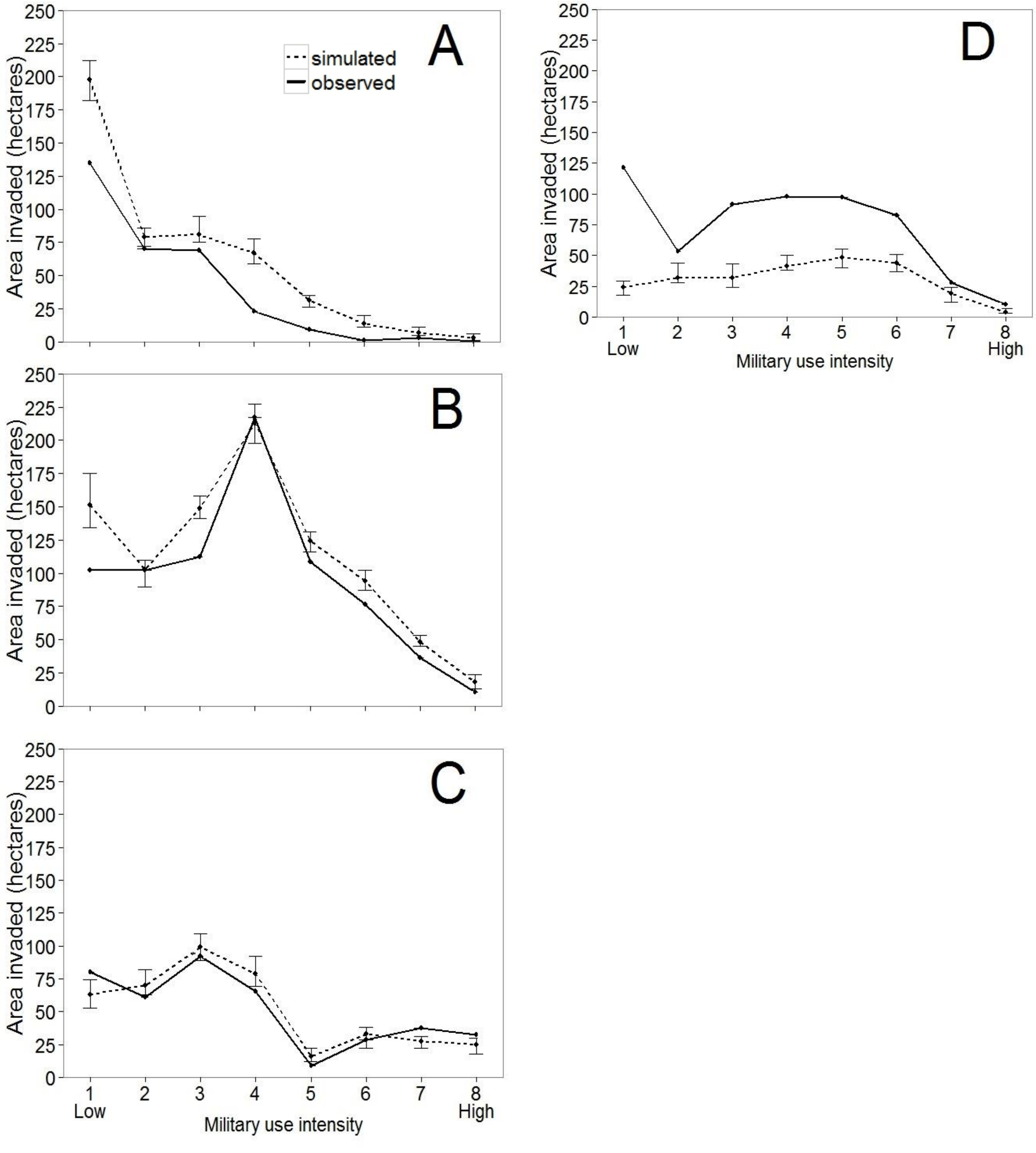


Figure 2.6: **A:** The observed and simulated values for Sericea invasion in A-grade prairies. **B:** The observed and simulated values for Sericea invasion in B-grade prairies. **C:** The observed and simulated values for Sericea invasion in C-grade prairies. **D:** The observed and simulated values for Sericea invasion in D-grade prairies. Error bars represent 95% confidence intervals for simulated values.

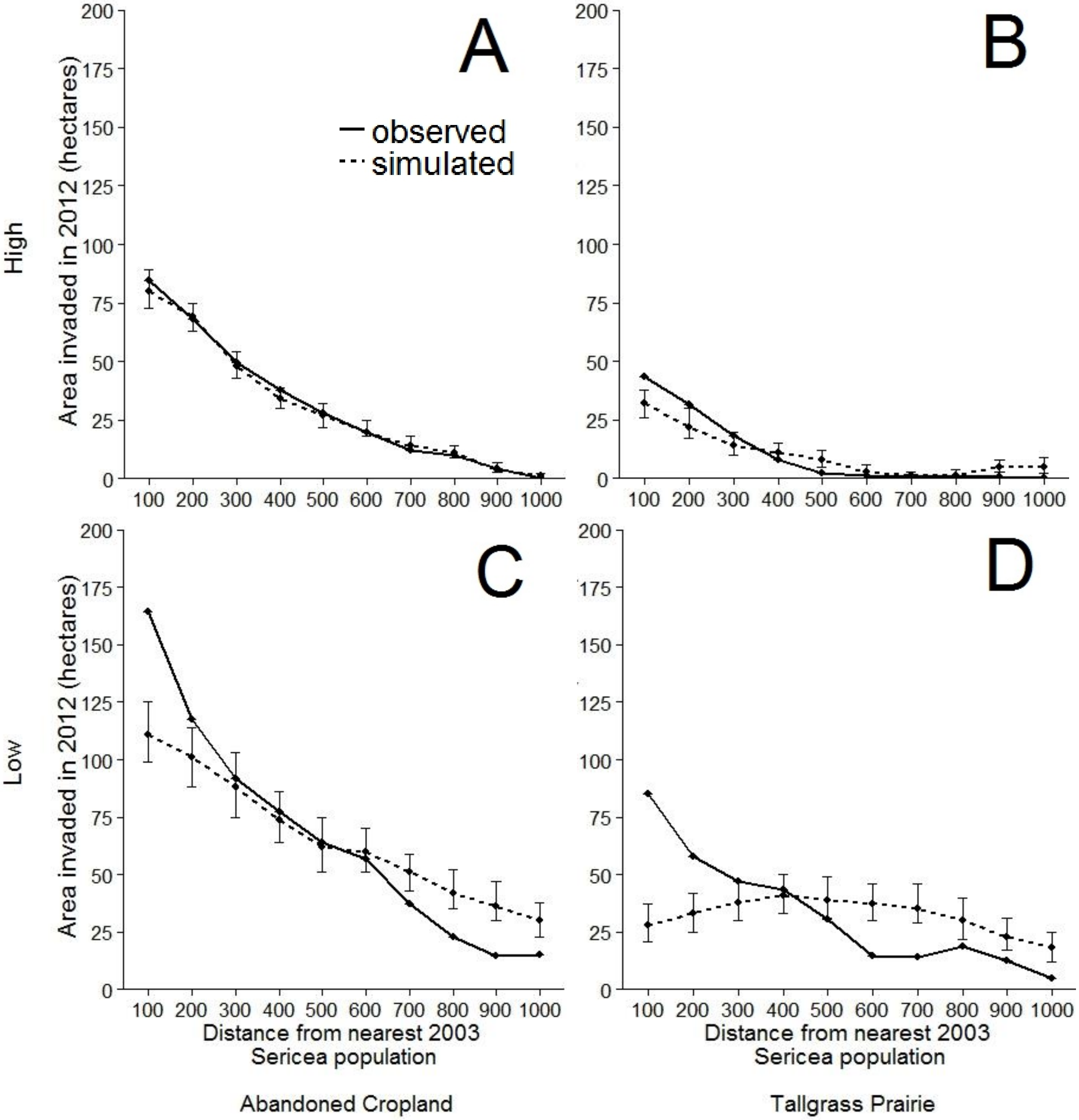


Figure 2.7: The area of tallgrass prairie and abandoned cropland invaded by Sericea between 2003 and 2011 ("observed") and simulated invasion totals ("simulated") assuming that all distances are equally likely to become invaded. **A.** The observed and simulated Sericea invasion in abandoned cropland under relatively high levels of military activity. **B.** Sericea invasion in tallgrass prairie under relatively high levels of military activity. **C.** Sericea invasion in abandoned cropland under relatively levels of military activity. **D.** Sericea invasion in tallgrass prairie under relatively low levels of military activity.

Figure 2.8: Photograph of an area of tallgrass prairie at FRMR where Sericea has become abundant in tank tracks.

# Chapter 3

## Restoring Land Heavily Invaded by Sericea Lespedeza (*Lespedeza cuneata*): testing hypotheses within community invasibility theory

## Abstract

Insights into the ability of natural communities to resist exotic invasion have generated interest in the use of restoration to bolster invasion resistance of degraded areas. While theory predicts that reestablishing competitive and diverse plant communities should reduce exotic invasion, it is unclear if restoration can be used to reduce the severity of invasion in already invaded areas. Furthermore, it is unclear what methods should be used for restoration or what attributes of the community should be restored to minimize the re-invasion of exotics. In this study, we examine how the methods used for tallgrass prairie restoration and how differences in the diversity and density of seed mixes affect the re-invasion of *Lespedeza cuneata* (Dum. Cours. G. Don; Sericea). We conducted experimental tallgrass prairie restorations in areas heavily invaded by Sericea. Restoration plots were prepared using either two applications of herbicide to kill living vegetation or one application of herbicide plus soil tillage. Native seed mixes were sown that varied in diversity and density. Additionally, one year after restoration, a subset of restoration plots received one follow-up application of herbicide to Sericea plants. Our results show that native tallgrass prairie can be established in areas heavily invaded by Sericea. Both Sericea cover and the number of flowering individuals are negatively affected by sowing restorations more densely, but increasing the diversity of seed mixes had no effect. Additionally, preparing the restoration site with mechanical tillage resulted in lower Sericea cover than sites prepared only with herbicide. When tallgrass prairie restoration is combined with follow-up herbicide application, Sericea cover is very low to non-existent and native cover is high. Sericea cover is increasing in our restorations that have not received follow-up herbicide, but it is unclear how abundant Sericea will become in these restorations in the future. Our results suggest that

restoring native grassland communities with high density seed mixes is more effective at resisting re-invasion of exotics than using high diversity mixes.

## Introduction

It is well known that the transport of exotic invasive species facilitated by humans is ecologically and economically problematic. Losses to biodiversity, crop production, and other economic activities have been well documented for animal and plant species (Pimental et al. 2005, Olson 2006, Lovell et al. 2006). Despite our understanding of mechanisms underlying invasion (for review see Richardson and Pysek 2006), invasive species are widespread (Pimental et al. 2005). Insights into the ability of natural communities to resist exotic invasion have generated interest in the use of restoration to bolster invasion resistance of degraded areas (Bakker and Wilson 2004, Funk et al. 2008, Foster et al. 2015). However, practitioners may find it challenging to use restoration to manage invasive species for multiple reasons. First, studies which investigate invasion mechanisms are conducted under highly controlled settings and at small scales (Tilman 1997, 1999), which may not reflect patterns of invasion on the large-scales at that practitioners operate (Levine 2000, Hierro et al. 2005). Also, methods often used for site preparation, seeding, and site maintenance in small-scale studies are not realistic at larger scales. We are also not aware of any study which explores whether restoring a site to its native state reduces the re-invasion of exotics on previously infested sites; a common circumstance for practitioners. In this study, we sought to advance the management of the noxious weed *Lespedeza cuneata* (Dum. Cours. G. Don; Sericea) by incorporating theory underlying the invasion resistance of plant communities into common restoration practices. More specifically, we assessed the potential of tallgrass prairie restoration (TPR) in combination with existing management practices to limit the re-invasion of Sericea on land previously invaded.

Sericea is an exotic legume that originates from eastern Asia and was first introduced into the U.S. in 1896 (Ohlenbusch and Bidwell 2001). Sowing Sericea was promoted for erosion control and wildlife habitat (Pieters 1950). In the Midwest, Sericea can become abundant in grassland communities and alter the composition of the resident plant community (Eddy and Moore 1998). Sericea is also problematic in agricultural fields because of its potential to decrease the value of grazing land (Fechter and Jones 2001). Sericea control has largely focused on reducing seed dispersal and controlling existing populations through the application of herbicides (Missouri Department of Conservation). While applying herbicide can effectively limit the size of Sericea populations (Koger et al. 2009), invaded areas often require ongoing herbicide application; which is expensive (Silliman and Maccarone 2005) and time consuming.

The ability of Sericea to easily reestablish following herbicide treatment may indicate an inherent susceptibility of some grassland systems to Sericea invasion. A study from Foster et al. (2015) showed that restoring abandoned agricultural land to native tallgrass prairie can greatly suppress the invasion success of Sericea compared to unrestored grassland for at least three years. This study demonstrated that Sericea establishment can be reduced if TPR is done prior to invasion. Unfortunately, it is difficult for land managers to justify the expense of TPR when they cannot anticipate if or when Sericea will invade. Many times, land managers do not initiate management efforts until after Sericea has already invaded. If TPR can confer resistance to re-invasion of Sericea on land already heavily invaded, incorporating it into current management practices could reduce the need for ongoing management.

Methods used for TPR to prevent Sericea's re-invasion on invaded land may be different than methods used when trying to prevent Sericea's initial invasion. Due to Sericea's prolific seed production (Woods et al. 2009), a substantial seed bank likely exists in established populations that, if not dealt with, could overwhelm the enhanced invasion resistance of TPR. Multiple rounds of herbicide applications or soil cultivations could be used prior to sowing native seed mixes in order to partially exhaust the seed bank. Since most viable seeds are likely near the soil surface, soil tillage may suppress Sericea reestablishment by burying seeds deeper than from which they can emerge (Qiu and Mosjidis 1993). However, tillage could also have the opposite effect by stimulating the seed bank and providing an ideal substrate for Sericea germination and growth. Stimulating the seed bank may also provide a brief opportunity for Sericea to easily reestablish following TPR because Sericea seedlings may not experience the same intense competition for resources (light, water, N) as when seeds germinate in established prairie communities. If this is the case, follow-up application of herbicide may be critical in suppressing Sericea growth until the sown, native community is established and can compete with Sericea seedlings.

While TPR may enhance the resistance of grassland to Sericea (Foster et al. 2015), we do not understand what aspects of the restored community confer invasion resistance. Because of this, it is unclear which species should be included in restoration seed mixes and at what densities they should be sown. One possible reason why TPR increases invasion resistance is that restored communities often have higher plant diversity than the disturbed communities. The diversity-invasibility hypothesis states that invasion resistance of a community increases as the number of species present increases (Elton 1958). It is thought that functionally dissimilar species utilize resources in a complementary fashion. Thus, functionally diverse plant communities should efficiently utilize resources, leaving resources unavailable to invaders. Species poor communities may have reduced resource uptake (Tilman 1996); possibly leaving resources available to invaders (Shea and Chesson 2002). Increasing plant diversity has been shown to increase the invasion resistance of plant communities in experimental studies (Tilman 1997, Naeem 2000, Kennedy et al. 2002). In addition to increasing plant diversity, TPR shifts the identity of abundant species toward $C_4$ (warm-season) grasses that may be more difficult for Sericea to out-compete. Studies have shown that in diverse communities, invasion resistance may be primarily determined by the identity of abundant species and not diversity per se (Grime 1998, Crawley et al 1999, Lepš et al. 2001, Wardle 2001, Smith et al. 2004). If TPR can be used to resist Sericea re-invasion, what seed mixes should be used in the restoration process to produce native plant communities that discourage the growth of Sericea: seed mixes with high diversity or seed mixes with fewer species, but higher densities of dominant competitive species?

This study is intended to: 1) test the role of the diversity and dominance of the restored plant community in regulating exotic re-invasion; and 2) provide some technical guidance for the potential implementation of TPR into current Sericea management by demonstrating the effectiveness of various restoration methods on Sericea re-invasion. To do this, we located areas of an abandoned hayfield in northeast Kansas that had been invaded by Sericea. In these areas, we implemented experimental tallgrass prairie restorations utilizing an incomplete factorial design that manipulates: 1) the methods used in site preparation; 2) the density and diversity of seed mixes; and 3) the use of follow-up herbicide application. All restoration plots were initially prepared with one round of herbicide to kill existing vegetation, and either a second round of herbicide or mechanical tillage prior to sowing. Seed mixes were designed to reflect what practitioners would realistically implement in a restoration setting. We used species and seeding rates based on the Conservation Reserve Program (CRP) guidelines for Kansas because CRP restorations are the most common type of TPR implemented on agriculturally disturbed land where Sericea tends to invade. Lastly, we assigned a subset of restoration plots to receive follow-up application of herbicide to Sericea in the second year following restoration. With this design, we answer the following questions:

1. What type of tallgrass prairie restoration seed mixes most effectively suppresses Sericea; those that are more diverse, or those that are seeded at higher densities?
2. How do differences in site preparation and the use of follow-up herbicide affect Sericea re-invasion?

If we see that Sericea cover is suppressed in plots initially prepared with tillage this may suggest that the burial of seeds may limit Sericea germination; whereas increases in cover in tilled restorations suggest a stimulating effect on the seed bank. Lower Sericea cover in diversely sown restorations would suggest that increased diversity of species within TPR confers invasion resistance. Alternatively, lower Sericea cover in densely sown restorations suggests that the abundance of prairie species in general is responsible for conferring invasion resistance.

## Methods

### *Study Site*

This study was initiated at The Hall Reserve of the University of Kansas Field Station (KUFS) which is which is located in northeastern Kansas (lat 39.01’N, long -95.35’W). This area of Kansas is within the prairie-forest ecotone region of the Midwest. Prior to KUFS managing the reserve, some areas had been reseeded to native prairie species in 1989 as a part of government conservation programs. After reseeding, these areas of the reserve were occasionally burned from 1990-1999 and from 2000-2004, and herbicide was occasionally applied to patches of Sericea. From 2005-2013, the site received minimal management. At the time this study was initiated in 2013, reseeded areas primarily consisted of native grasses and a few forb species including: Indian grass (*Sorghastrum nutans;* L.) Nash, big bluestem (*Andropogon gerardii;* Vitman), maximillian sunflower (*Helianthus maximiliani;* Schrad), and showy partridge pea (*Chamaecrista fasciculate;* Michx.). Reseeded areas were also heavily infested with Sericea. Of the 84 experimental plots established for this study (see below), 28 were established in areas that had been reseeded. One of the sites within the reseeded areas likely sustained substantial disturbance by bulldozer activities in the 1950s. The rest of the reserve, where the remaining 56 plots were established, was managed similarly, with the exception of not receiving native seed additions. Vegetation in the non-reseeded areas were dominated by brome (*Bromis inermis;* Leyss; an exotic $C_3$ grass), broomsedge (*Andropogon virginicus* L.; an opportunistic $C_4$ grass ), and Sericea.

### *Experimental Design*

We were interested in testing how alternative strategies for TPR affected Sericea re-invasion on heavily invaded land. To accomplish this, in June of 2013, we established 84 10 x 3 m plots in areas of the reserve heavily invaded by Sericea. We applied an incomplete factorial arrangement of treatments to these plots. Treatments were comprised of four experimental factors, each with two levels: site preparation (SITE PREP: till or herbicide); SEED MIX DIVERSITY (high diversity and low diversity); SEED MIX DENSITY (high density and low density); and post-restoration follow-up herbicide application (SPRAY: follow-up herbicide applied, and no follow-up herbicide applied). Fully crossing all four factors would have produced 16 unique treatment combinations. However, because the number of suitable sites for restoration was very limited in 2013, we only established 84 total restoration plots, which resulted in an incomplete factorial design of our experiment with 14 unique treatments (6 replicates each; Table 3.1). The herbicide x low density x high diversity x sprayed and the till x low density x high diversity x sprayed combinations were not implemented in the final design. Both of these treatment combinations were excluded because we wanted to maintain the ability to test for potential interactions between the SITE PREP, SEED MIX DENSITY and SEED MIX DIVERSITY treatments. Also, we were unable to locate all plots in the same general area. Plots were located in parts of the reserve where Sericea had invaded naturally. There were not enough large invaded areas within the reserve to accommodate a blocked design so each plot was randomly assigned to one of the 14 treatment combinations. Twenty-eight plots were located in areas of the reserve that had been seeded to native tallgrass prairie species, while the remaining 56 plots were established in other areas of the reserve. In the reseeded area, ten plots were sown with low diversity-high density seed mixes; six of these SITE PREP = till and four SITE PREP = herbicide. Four plots were sown in the reseeded area with low diversity-low density seed mixes; two of these SITE PREP = tilled and two SITE PREP = herbicide. Five plots were sown in the reseeded area with high diversity-low density seed mixes; three of these SITE PREP = tilled and two SITE PREP = herbicide. Nine plots were sown in the reseeded area with high diversity-high density seed mixes; four of these SITE PREP = tilled and five SITE PREP = herbicide). In our design, we did not include control plots that received no intervention or plots restored with non-native species because these controls are not viable restoration strategies. Furthermore, we did not treat infestations using only spot spraying because this management strategy had been studied previously (Koger et al 2009).

On June 3, 2013, after restoration plots were marked, but prior to the application of the experimental sowing treatments, all plots (0.62 acres) were sprayed with an herbicide mix containing three fl oz glyphosate/gal and two fl oz tryclopyr /gal of (27 gal. of mixture total). Seven days after herbicide was applied, dead vegetation was removed from all plots with a weed whacker and rake, which left very short vegetation stubble and bare ground. Plots were left for thirteen days to allow the seed bank to germinate and regrowth to occur. From June 23-July 8, we prepared the sites to receive the seed mixes. SITE PREP (two levels: till and herbicide): After vegetation was removed, half of the plots were tilled using a tractor mounted rototiller to simulate plowing and disking (till) and half were sprayed with the herbicide mixture (described above) a second time (herbicide). All plots in the experiment were lightly disked to improve sown species seed germination. On July 9, after completing site preparation, plots were seeded with one of four unique seed mixes that varied in diversity and density (seeds purchased from Stock Seed Farms, Murdock, NE U.S.A). SEED MIX DIVERSITY (two levels: high diversity and low diversity): seed mixes contained either fifteen (low diversity) or thirty plant species (high diversity) selected from the Kansas CP25 tallgrass prairie guidelines (Table 3.2). SEED MIX DENSITY (two levels: high density and low density): plots were sown at densities equal to what was suggested under CP25 guidelines (26 lbs. PLS total/acre) (low density) or double (52 lbs. PLS total/acre) the suggested density (high density). SPRAY (two levels: follow-up herbicide applied, no follow-up herbicide applied): in June 2015 (two growing seasons after restoration), a subset of restoration plots were spot sprayed using a backpack sprayer with two fl oz tryclopyr/gal mixture while the remaining plots received no follow-up herbicide Spot spraying effort was held constant by spending exactly five min. spraying in each plot

### *Data collection*

In July of 2014 and 2015, cover surveys were conducted by randomly placing two, 1m$^2$ quadrats within each plot and estimating the absolute cover of every species identified within the quadrats. Total cover values were allowed to exceed 100% to account for plant cover present in multiple levels of the plant canopy. In addition to our cover survey in June 2015, we estimated

Sericea cover and counted the number of flowering Sericea individuals in September 2015. We also estimated mean height of Sericea individuals within each quadrat. Mean height was estimated by randomly selecting individuals within the quadrat area of the June cover survey and measuring the height of the tallest branch of each individual. A maximum of ten individuals were measured in each quadrat. However, many plots had fewer than ten individuals. In some cases, no plants were found in one of the two quadrats so mean height was averaged using plants in only one quadrat.

### *Data Analysis*

For the purpose of our analyses, the aggregate of all sown species within each quadrat is referred to as “sown cover”. The cover of all species (sown and non-sown) is referred to as “total cover”. Species percent covers, height of Sericea individuals, and number of flowering Sericea individuals were averaged within each plot resulting in one value for each plot. Response variables used to assess effects of the treatment factors on the sown community were total cover (including Sericea), sown cover, non-sown cover, forb cover, $C_4$ grass cover, bare ground, litter, sown species Shannon diversity, and sown species richness (Table 3.3). Response variables used to assess treatment effects on Sericea re-invasion included Sericea cover, Sericea height, and number of flowering Sericea individuals.

To examine the effects of our treatments on sown community establishment and Sericea cover, we performed two fully factorial ANOVAs on separate subsets of the treatment combinations because all factors were not fully crossed. ANOVA (I) was performed to examine the main and interactive effects of SITE PREP, SEED MIX DIVERSITY, and SEED MIX DENSITY only in plots that did not receive the follow-up herbicide (SPRAY) treatment (Table

3.1). ANOVA II was performed to examine the main and interactive effects of SITE PREP and SPRAY only in plots that were seeded with the high density, high diversity seed mix (Table 3.1). Despite the SITE PREP treatment only being fully crossed with the low diversity level of the SEED MIX DIVERSITY treatment, high and low-density plots and high and low-diversity plots were pooled together for analysis because we found no main effect of SEED MIX DIVERSITY in ANOVA I. The incomplete factorial design did not allow us to test interactions between the SPRAY treatment and the SEED MIX DIVERSITY and SEED MIX DENSITY treatments.

ANOVA I was used to test treatment effects on seven of the nine community establishment variables including total plant cover, total sown cover, non-sown cover, grass cover, Shannon diversity of sown species, sown species richness, and litter. Assumptions for ANOVA were checked by visualization of residuals and by using the Bartlett test to check for heteroschedasticity. A log transformation was applied to sown cover, litter, and non-sown cover in community response variables to correct for heteroschedasticity. The location of restoration plots was included in ANOVA I of sown community establishment (located in native reseeded area or a non-reseeded area) to control for possible effects of past disturbance or the prior vegetation type. Mann-Whitney U tests were used to test the remaining two community establishment variables: percent bare ground and percent forb cover because response variables did not meet the assumption of homoscedasticity. ANOVA II was not used to test treatment effects on community response variables because it was unlikely that follow up application of herbicide would cause changes in the sown community as non-target casualties were very uncommon.

ANOVAs I and II were also used to test the effects of the treatments on Sericea cover and height. Because Sericea cover was measured twice (June 2015, and September 2015), repeated measure ANOVAs were used to test treatment effects on Sericea cover. A log plus 1 transformation was used for percent of Sericea cover because of its deviation from a normal distribution due to numerous zero values. The plot location factor was left out of ANOVA (II) tests because not all treatment combinations of the SPRAY factor were present in the reseeded area of the reserve.

To determine if the density and diversity of seed mixes affected Sericea flowering, a Chi-square test was performed on the total number of flowering individuals in each unique sowing treatment. All figures and statistical tests were completed in R statistical software 3.0.2 utilizing the “vegan”, “car” and “ggplot2” packages.

## Results and Discussion

### *Sown Community Establishment*

Sowing treatments significantly affected total cover, sown cover, non-sown cover, grass cover, forb cover, litter, sown plant richness, and sown plant diversity (Table 3.3). Densely sowing restoration plots did not significantly increase total sown cover as we expected it would, but did lower non-sown cover which in turn, significantly reduced total plant cover (including Sericea cover). It is possible that in densely sown restorations, greater initial density of sown species suppressed the establishment of non-sown species, but the greater density did not result in greater sown cover. Low diversity restorations have higher sown cover and grass cover than those seeded with high-diversity mixes. This is likely because low diversity seed mixes contained higher amounts of $C_4$ grass species that typically establish easily including: *Sorghastrum nutans* (*S. nutans) Andropogon gerardii (A. gerardii), Schizachyrium scoparium (S. scoparium),* and *Panicum virgatum (P. virgatum*). To maintain equal seed densities in high and low density seed mixes, diverse seed mixes (which have twice the number of species) have half the seed of easily establishing species than the low diversity mix. Some species (particularly grass species) present only in diverse mixes did not establish well (Figure 3.1) resulting in lower sown cover in restorations seeded with diverse mixes (Table 3.3). Forb cover was slightly higher in restorations sown with diverse seed mixes (Table 3.3) because, unlike the grass species included in high diversity seed mixes, forb species included in high diversity mixes established nearly as well as forb species included in the low diversity mixes (Figure 3.1). Species diversity (*H'*) is higher in high-diversity restorations, but the effect is modest. Interestingly, restorations sown with high density mixes have significantly higher sown species richness than their low density counterparts, but the diversity of the seed mix had no effect on richness (Table 3.3). If some species seeded in our restorations are less likely to establish (such as relatively conservative forbs), then the higher number of seeds present in densely sown restorations may have increased the likelihood of those species being present; producing communities with slightly higher richness. However, the abundance of these species is likely low considering the diverse seed mixes led to more diverse plant communities, but the density of the seed mix had no effect on diversity. Litter was not affected by any of our seed mix treatments, but was significantly lower in sites prepared with herbicide only compared to those prepared with tillage (not shown). Interestingly, there is a significant effect of the location of restoration plots on total cover, sown cover, non-sown cover, and litter. Restoration plots located in an area of the field that had been previously seeded to native vegetation had significantly less total cover than plots that were not seeded to natives. Because all of the plots sown in previously native vegetation were concentrated in one area, previous vegetation type and their topographic location are confounded. There may have been substantial soil disturbance created by bulldozer activity in the 1950’s which could have degraded the soil quality and may have lowered sown species establishment.

### *Effects on Sericea re-invasion*

In ANOVA I, Sericea cover was significantly affected by the SEED MIX DENSITY and SITE PREP. While there was no significant main effect of SEED MIX DIVERSITY, there was a significant four-way interaction that included SEED MIX DIVERSITY. Restorations sown with more dense seed mixes had significantly lower Sericea cover than those sown with their less dense counterparts (ANOVA I; Figure 3.2c and d). Sowing restorations with more diverse mixes did not affect Sericea cover (Figure 3.2c and d). Restorations prepared with soil tillage have significantly lower Sericea cover than those prepared with herbicide only (SITE PREP; Figure 3.2a and b, c and d). We saw a significant increase in Sericea cover between the surveys in June and September (TIME; Figure 3.2a and c, b and d). ANOVA I also showed a significant four-way interaction between all factors (SITE PREP, SEED MIX DENSITY, SEED MIX DIVERSITY, and TIME). This interaction seems to indicate an effect of diversity, but only under particular circumstances. Seed mixes with higher diversity suppressed Sericea cover only in September, only when using low density seed mixes, and only in restorations prepared with herbicide only.

In ANOVA II, follow-up herbicide application (SPRAY) resulted in significantly lower Sericea cover (ANOVA II; Figure 3.3a and b) and its absolute effect on Sericea cover was much larger than any other treatment. While all restorations experience some increase in Sericea cover between June and September surveys (ANOVA II: TIME; Figure 3.3a and b), restorations that received follow-up spray experienced very little absolute change in Sericea cover between June

(Figure 3.3a) and September surveys (Figure 3.3b). Restorations that were not sprayed experienced large increases in Sericea cover. This led to a large difference in the effect of SPRAY over time resulting in a significant interaction between SPRAY and TIME.

Sericea height was not significantly affected by SEED MIX DENSITY, SEED MIX DIVERSITY, or SITE PREP (ANOVA I; Figure 3.4a & b), but was significantly lower in restorations that received follow-up herbicide (SPRAY; ANOVA II; Figure 3.5). Follow-up herbicide application likely reduced the mean height of Sericea by selectively removing taller individuals from the community that were more visible at the time of spraying. Follow-up herbicide application drastically reduced the number of flowering individuals. Of the 245 flowering Sericea individuals counted within all restoration plots, only six were located in plots which received follow-up herbicide (not shown). The effect of follow-up herbicide application on flowering individuals was so dramatic that we did not subject it to any statistical tests. When we examined the effects of our seed treatments on Sericea flowering, we found that restorations sown with dense seed mixes had fewer flowering individuals than their low density counterparts and lower than would be expected by chance (Figure 3.6). While there are slightly more flowering individuals in the high-diversity, low-density seeding treatment than would be expected by chance, there are many fewer in this treatment than in the low-diversity, low-density treatment.

The suppressive effects of SEED MIX DENSITTY on Sericea cover and flowering individuals occurred despite there being no significant difference in total sown cover between our two density treatments. It is possible that densely sown restorations resulted in a higher density of sown species in the initial stages of germination and growth relative to less dense treatments and may have created low light conditions that hindered Sericea seedling growth

(Mosjidis 1990) early on. These initial differences in sown species could have diminished as dominant species became abundant and prior to our first cover surveys, but differences in the suppressive effects on Sericea remain. The limited effects of SEED MIX DIVERSITY (only in restorations sown at low density and prepared with herbicide only; Figure 3.2c) on Sericea establishment could be due to the poor establishment of species specific to the diverse seed mixes. Species unique to our diverse seeding treatment only contribute 9.3% of the total absolute cover to diverse restorations whereas species common to all seed mixes account for 58.9%. If increased diversity of prairie species generally enhances the invasion resistance of tallgrass prairie, the modest increase in diversity achieved in this experiment may not have been enough to affect Sericea invasion.

The lower Sericea cover and fewer flowering individuals in densely sown restorations suggest that suppressive effects of higher seed densities (and presumably higher number of plants) of species especially dominant grasses (*A. gerardii, S. nutans,* and *P. virgatum*) may be more effective than greater numbers of species at limiting Sericea establishment and growth. This is consistent with the idea that the higher observed invasion resistance of tallgrass prairie to Sericea documented in Foster et al. 2015 may be due largely to dominance by a few highly competitive species and not diversity per se. Despite no difference in the $C_4$ grass abundance among our sowing treatments, the suppressive effect of $C_4$ grasses may be important in resisting invasion. Smith et al. (2004) found that manipulations of richness did not affect invasion by the invasive biennial legume, *Melilotus officinalis*, but experimentally altering the abundance of dominant grasses species within the recipient community did. The lack of diversity effects in our study and in Smith et al.'s doesn't necessarily undermine the diversity-invasibility theory, but may illustrate the practical challenge of establishing plant diversity high enough to increase invasion resistance. In our study, we intentionally designed seed mixes under practical and financial constraints that many practitioners likely encounter when performing restorations. Under these constraints, increasing plant diversity was difficult; as seen in our results. Others have demonstrated a suppressive effect of $C_4$ grasses on native forbs (Camill et al. 2004, Dickson and Busby 2009), some of which can grow and spread vigorously. The negative relationship between dominate native grasses and forbs generally, may indicate the potential of $C_4$ grasses to also displace invasive forb species such as Sericea.

Absolute differences in Sericea cover between site preparation methods (pre-restoration herbicide versus tillage) became larger as the growing season progressed. By preparing restoration sites with herbicide only, some Sericea individuals may have survived due to incomplete herbicide coverage across the restoration area. Surviving Sericea plants likely grow more quickly from living root systems compared to plants germinating from the seed bank, resulting in higher Sericea cover in plots prepared with herbicide only. Mechanical tillage prior to restoration may have prevented some Sericea seeds from germinating by burying them deeper than seedlings can emerge from (Moore, 1943). There was a significant interaction between the SPRAY and TIME (Figure 3.3). This is likely an indication of the non-linear growth of Sericea over the growing season. Plots with little Sericea present (till prep-follow-up spray) saw minimal growth, but restorations with many individuals present (herbicide prep-no follow-up spray) experienced a tremendous amount of growth over the course of the growing season.

Follow-up herbicide had the largest impact on Sericea cover among our treatments, confirming the effectiveness of herbicide seen previously in other studies (Koger et al. 2009). Follow-up herbicide greatly decreases Sericea cover, regardless of the site preparation and seed mix used for restoration. The mean Sericea cover of all plots that received follow-up herbicide in

September 2015 was only 1.9% compared to 15.7% in plots which received no herbicide. Follow-up herbicide may be particularly important in minimizing the chance of high Sericea cover. The highest amount of Sericea observed among sprayed plots was just over 10% compared to over 60% in plots which did not receive herbicide (not shown). Follow-up herbicide also significantly reduced the mean height of Sericea individuals within restoration plots. This may result from the unintentional selective spraying of larger, more visible plants. By removing larger plants, follow-up herbicide also drastically reduced the number of reproductive plants. The dramatic reduction of reproductive plants may reduce the amount of ongoing management needed in the future by reducing seed entering the seed bank.

Determining which types of management interventions to implement for invasive species control requires careful consideration of management goals. If land is invaded by Sericea and TPR is desired, it is possible to establish native tallgrass prairie and also reduce the abundance of Sericea. However, the exact methods used for restoration should be dictated by the goals of the restoration. If forb species are not desired, the most effective strategy for managing Sericea may be to densely sow a seed mix composed of vigorous grass species. Then, after Sericea plants emerge from the plant canopy, apply tryclopyr herbicide over the entire area. Broadcast application of herbicide is likely more cost-effective for even modestly sized restorations compared to the roughly 11.2 h/ac required to apply herbicide with a backpack sprayer as was done in our study. Alternatively, if a diverse forb community is desired in areas invaded by Sericea, extensive spot application of herbicide following restoration will be necessary to ensure that Sericea does not reestablish. Although we did not find any benefit in adding diversity to the seed mix, more research on this question is warranted. Our high diversity seed mix only increased diversity modestly and we cannot say whether or not seed mixes with much larger proportions of forb seed and/or higher diversity of seed would be effective in controlling Sericea reestablishment.

The site preparation strategies used in our study could be modified by practitioners to further limit Sericea reestablishment. Our attempt to exhaust the seed bank via herbicide application or tillage prior to planting was likely not fully effective. The period of time between the first and second round of site preparation occurred in July, which was unseasonably hot and dry, and likely resulted in very little seed germination in the seed bank. To further exhaust the seed bank, it may be prudent to wait a longer period of time to allow the seed to germinate from the seed bank. This strategy could be repeated several times over the course of a full growing season prior to sowing native mixes.

Many of our treatment combinations resulted in Sericea cover many would consider below nuisance levels. In untreated areas adjacent to our restoration plots, Sericea cover is extremely dense and likely approached 100% in September of 2015 (Figure 3.7) compared to much lower Sericea cover in restored plots. Furthermore, the average cover of Sericea across all plots prior to restoration was 29.1% in June 2013 and was reduced to an average of 2.88% across all treatment combinations in June 2015; a relative reduction of 90.1% (not shown). However, there are two aspects of our study that should be considered when applying our findings in the field. The first is that we cannot determine the relative effectiveness of our methods here compared to methods that do not include TPR. It is not clear how seeding cool season grass species, instead of native prairie species would affect the re-invasion of Sericea. We also do not know whether or not invaded areas which have undergone TPR will maintain low levels of Sericea cover into the future without further management. Because our study only follows Sericea reestablishment two years following restoration, we cannot say with reasonable certainty that TPR will effectively suppress Sericea over long periods without follow-up application of herbicide.

There has been growing interest in the use of restoration to reduce exotic species invasion. However, the quality of many areas has already been compromised by invasive species and it is unclear whether restoration can be used to lessen the impact of invasive species on already invaded land. This is the first study, to our knowledge, that examines the potential use of tallgrass prairie restoration for the remediation of exotic plant invasion. We have shown that tallgrass prairie restoration can be used in conjunction with current management strategies to successfully reestablish native prairie vegetation and limit the re-invasion of Sericea.

## Tables and Figures

Table 3.2: All treatment combinations in the experiment. The two treatment combinations shaded in grey were never implemented because of the incomplete factorial design of the experiment. “ANOVA I” and “ANOVA II” columns indicate what treatment combinations were included in each ANOVA for tests of the characteristics of the sown community, Sericea cover, and Sericea height. For the SITE PREP, plots were either prepared with one round of herbicide and one round of tillage (till) or two rounds of herbicide (herbicide) prior to sowing seed mixes. For the SPRAY treatment, plots were either receive one application of herbicide one year following restoration (sprayed) or did not receive herbicide (not sprayed)

| ANOVA I | ANOVA II | SITE PREP | SEED MIX DENSITY | SEED MIX DIVERSITY | SPRAY |
|---|---|---|---|---|---|
|  | I | till | high | high | sprayed |
| I | I | till | high | high | not sprayed |
|  | I | till | high | low | sprayed |
| I | I | till | high | low | not sprayed |
|  |  | till | low | high | sprayed |
| I | I | till | low | high | not sprayed |
|  | I | till | low | low | sprayed |
| I | I | till | low | low | not sprayed |
|  | I | herbicide | high | high | sprayed |
| I | I | herbicide | high | high | not sprayed |
|  | I | herbicide | high | low | sprayed |
| I | I | herbicide | high | low | not sprayed |
|  |  | herbicide | low | high | sprayed |
| I | I | herbicide | low | high | not sprayed |
|  | I | herbicide | low | low | sprayed |
| I | I | herbicide | low | low | not sprayed |

Table 3.3: All of the sown species included in the experiment are shown including their common names. Also, we have included the seeding rates of all species in the high diversity and low diversity treatments. While the seeding rates of species are not given for the high density treatment, they are all double of the rates shown.

| Species | Common name | Seeding rate (PLS/acre)* |
|---|---|---|
| High diversity only | | |
| *Liatris pcynostachya* | Blazing star | 0.1 |
| *Elymus canadensis* | Canada wild rye | 3 |
| *Achillea millefolium* | yarrow | 0.1 |
| *Dalea purpurea* | purple prairie clover | 0.1 |
| *Echinacea pallida* | pale purple coneflower | 0.1 |
| *Eragrostis trichodes* | sand lovegrass | 3 |
| *Festuca ovina* | sheep fescue | 3 |
| *Medicago sativa* | alfalfa | 0.1 |
| *Monarda fistulosa* | wild bergamot | 0.1 |
| *Ratibida pinnata* | gray-headed coneflower | 0.1 |
| *Sporobolus cryptandrus* | sand dropseed | 3 |
| *Symphyotrichum novae-angliae* | New England aster | 0.1 |
| *trifolium pratense* | red clover | 0.1 |
| *trifolium repens* | white clover | 0.1 |
| *Tripsacum dactyloides* | eastern gamagrass | 2 |
| High diversity and Low diversity | | |
| *Amorpha canescens* | lead plant | 0.1 |
| *Andropogon gerardii* | big bluestem | 6 |
| *Asclepias tuberosa* | butterfly milkweed | 0.1 |
| *Bouteloua curtipendula* | sideoats gramma | 6 |
| *Dalea candida* | white prairie clover | 0.1 |
| *Desmanthus illinoensis* | Illinois bundleflower | 0.1 |
| *Echinacea purpurea* | purple coneflower | 0.1 |
| *Helianthus maximiliani* | maximilian's sunflower | 0.1 |
| *Lespedeza capitata* | round-headed bushclover | 0.1 |
| *Panicum virgatum* | switchgrass | 4 |
| *Ratibida columnifera* | upright prairie coneflower | 0.1 |
| *Rudbeckia hirta* | black-eyed-susan | 0.1 |
| *Salvia azurea* | blue sage | 0.1 |
| *Schizachyrium scoparium* | little bluestem | 3 |
| *Sorghastrum nutans* | indian grass | 6 |

Taxonomy follows USDA plant database (https://plants.usda.gov) * Species included in the high diversity and low diversity treatments are indicated in the heading shown in the "Species" column. Seeding rates for each species in the high density treatments were simply double of the seeding rates shown

Table 4.3: Results of ANOVA I testing native community attributes (Mean ± 1 SE).

| Community characteristics in June 2015 | Significant Factors | Low Diversity | | High Diversity | |
|---|---|---|---|---|---|
| | | Low Density | High Density | Low Density | High Density |
| Total cover (%) | density*, location*** | 115.9±11.2 | 103.7±14.3 | 108.2±14.3 | 96.7±8.6 |
| Sown cover (%) | diversity*, location*** | 78.9±12.8 | 82.1±14.9 | 65.1±12.9 | 67.8±10.4 |
| Non-sown cover (%) | density***,location* | 40.8±4.1 | 22.7±1.9 | 46.6±5.83 | 30.0±2.5 |
| Forb cover (%)† | diversity** | 7.6±0.9 | 7.8±0.8 | 9.6±0.9 | 11.4±0.5 |
| C4 grass cover (%) | diversity** | 71.2±6.1 | 74.2±6.3 | 55.4±5.7 | 56.4±4.3 |
| Bare ground (%)† | not significant | 11.0±3.8 | 10.3±5.0 | 13.1±6.4 | 14.3±5.6 |
| Litter (%) | site prep***, site prep x location *** | 36.5±7.0 | 37.0±7.8 | 29.2±5.7 | 35.7±8.3 |
| Sown species diveristy (H') | diversity*, density x site prep* | 1.61±0.07 | 1.6±0.12 | 1.6±0.11 | 1.7±0.08 |
| Sown species richness (S) | density** | 8.7±0.81 | 10.6±0.43 | 9.1±0.96 | 10.5±0.61 |

Combined results from ANOVA which included SITE PREP ("site prep"), SEED MIX DENSITY("density"), SEED MIX DIVERSITY ("diversity") and if plots were located in areas previously seeded with natives or not ("location") and the mean±SE. * $P < 0.05$, ***$P < 0.001$. † Tests did not meet the normality assumption of ANOVA and were tested using Mann-Whitney U comparisons.

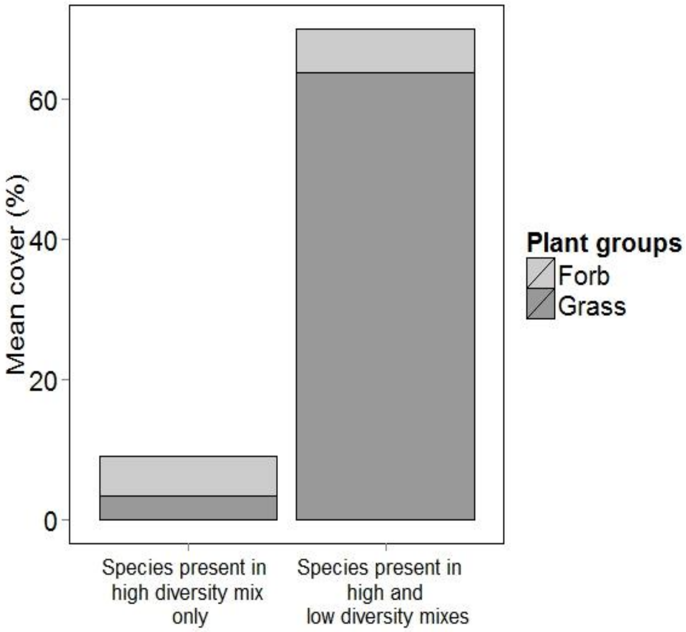


Figure 3.1: The mean absolute abundance across all experimental plots of species that were sown in the high diversity and low diversity seed mixes; and those that were only sown in plots assigned to the high diversity seeding treatment.

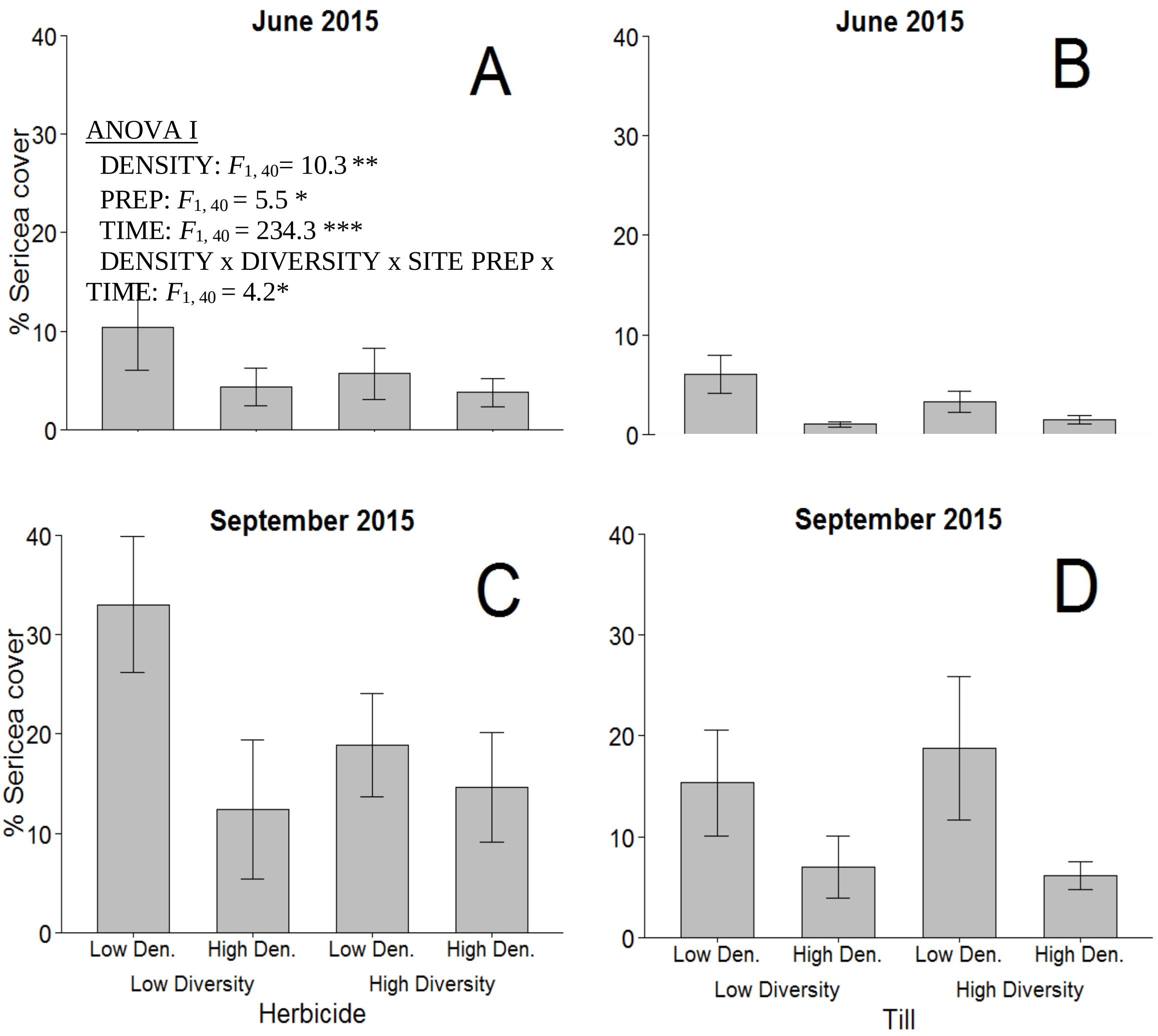


Figure 3.2: Mean Sericea cover ± 1 SE of unique treatment combinations included in repeated measures ANOVA I (PREP x SEED MIX DENSITY x SEED MIX DIVERSITY). Panes are organized by PREP treatment and by the time that surveys were taken in 2015. Restoration plots prepared with herbicide only are in the left column (A & C), plots prepared with mechanical tillage are in the right column (B & D). Results of surveys done in June 2015 are shown on the top row (A & B) and results from September 2015 surveys are shown in the bottom row (C & D). Significant ANOVA results of are presented in panel A. Results are from the overall model, not just to cover measurements taken in June 2015. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

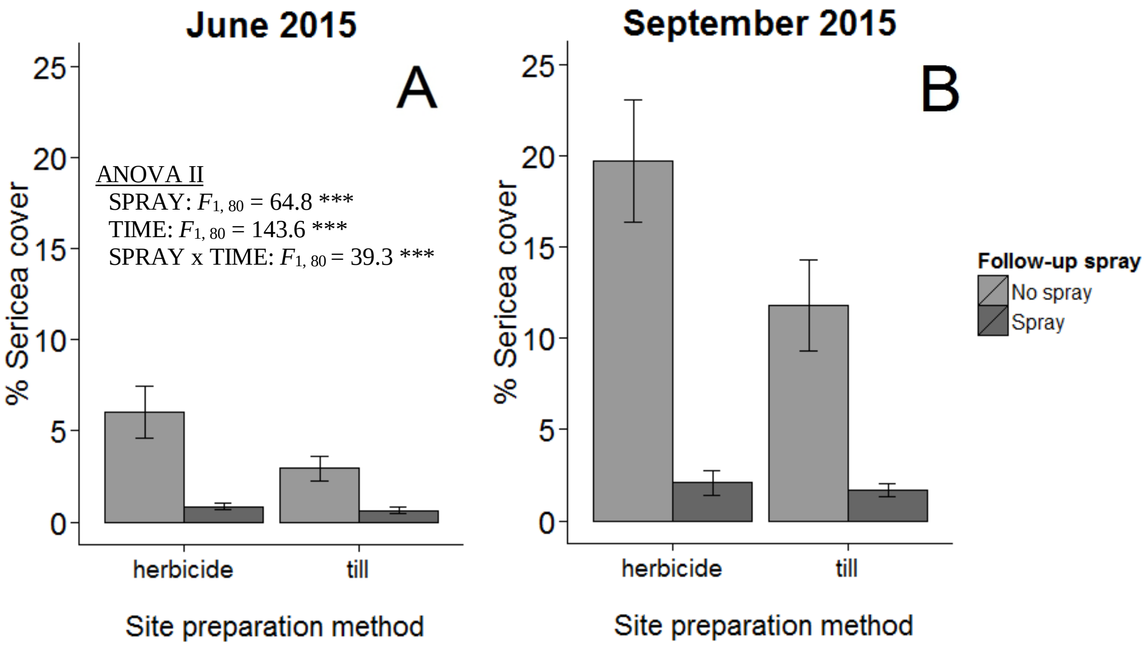


Figure 3.3: Sericea cover ± 1 SE of treatment combinations tested with repeated measures ANOVA II (PREP x SPRAY) Results of ANOVA II are presented in panel A. The "herbicide" treatment indicated on the x axis refers to the site preparation method used to remove existing vegetation and "spray" referred to in the legend refers to follow-up application of herbicide used after restoration were seeded and became established.

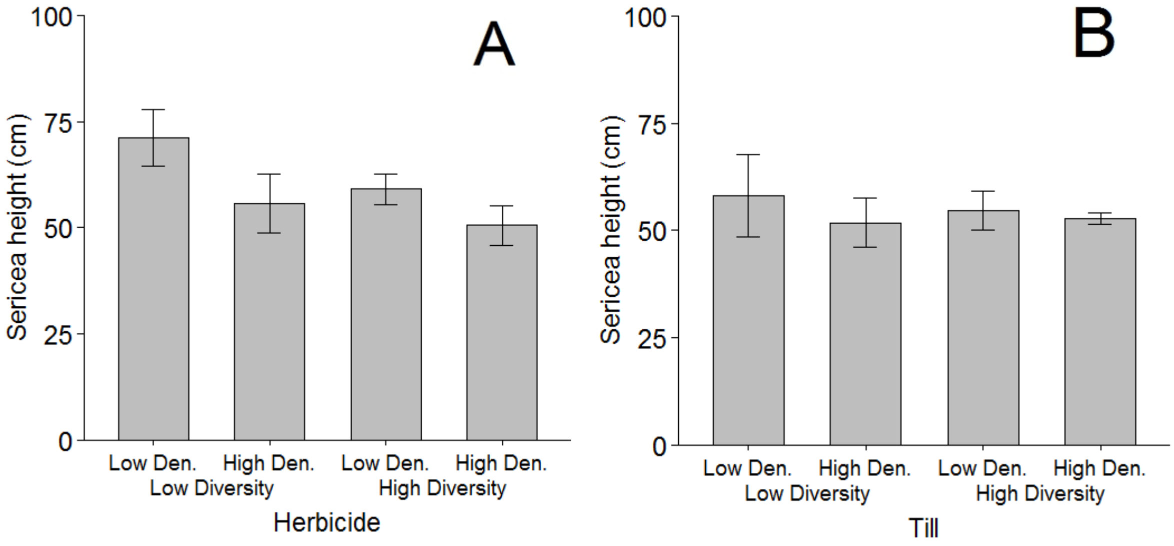


Figure 3.4: Mean Sericea height ± 1 SE in restoration plots differentiated by PREP, SEED MIX DIVERSITY, and SEED MIX DENSITY treatment combinations; the same treatments tested in ANOVA I. **A:** Treatment combinations within the Herbicide PREP treatment. **B:** Treatment combinations within the till PREP treatment. There were no significant effects of PREP or SPRAY in ANOVA I for Sericea height so none are shown.

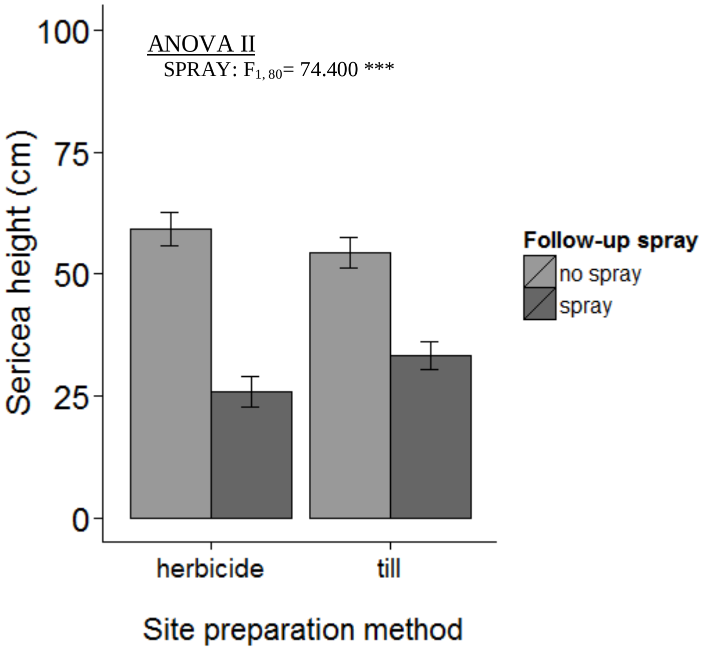


Figure 3.5: Mean Sericea height ± 1 SE in restoration plots differentiated by PREP, and SPRAY treatment combinations; the same treatments tested in ANOVA II. Significant results are presented in the figure. *** $P < 0.001$.

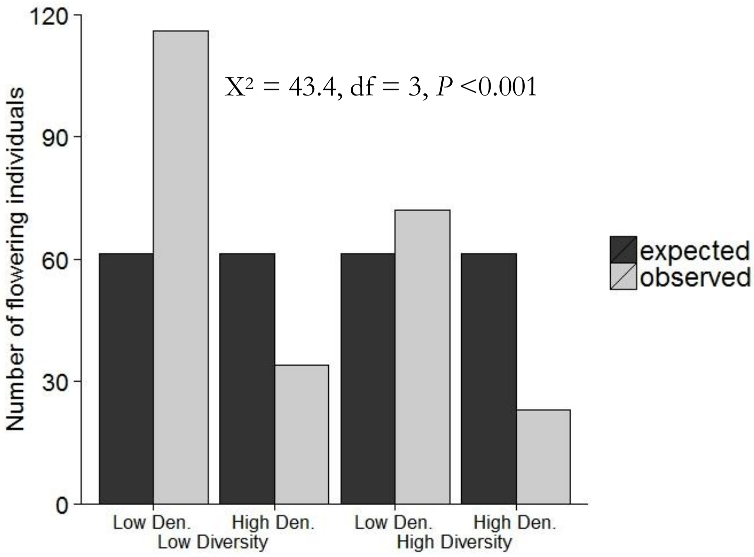


Figure 3.6: The expected and observed number of flowering individuals in the SEED MIX DENSITY and SEED MIX DIVERSITY treatments.

Figure 3.7: The border is shown between a restoration plot marked by PVC (right) and heavily invaded field surrounding it (left). This is a very common site among restoration plots. This restoration plot has a particularly high cover of P. virgatum (Switchgrass).

# Conclusions

This dissertation generally explores the processes regulating the species abundances within tallgrass prairies. Each chapter of this dissertation uses ecological theory as a foundation from which to design experimental restorations and to conduct large-scale observational studies that may improve prairie restoration and management. In chapter 1, our spatially manipulated restorations were designed to evaluate the effects of initial spatial structure on the establishment and persistence of sown prairie species over the long-term. The aim was to evaluate aspects of spatial coexistence theory, while also assessing the potential utility of spatial planting strategies for community restoration. We wanted to address the long-standing difficulty in re-establishing diversity in prairie restorations caused by the dominance of a few native species. Chapters 2 and 3 refined our understanding of the factors that influence exotic plant invasion and sought to improve the control of the invasive species *Lespedeza cuneata* (Sericea); that commonly invades and degrades grassland communities. In these chapters, we explored how the features of grassland communities, disturbance, and propagule pressure influence Sericea invasion.

The results in chapter 1 illustrated that the initial spatial structure of the plant community affects the composition of the community by affecting the abundances of aggressive, fast growing species. We showed that aggregated spatial structures that theoretically should lead to more diverse communities and improved restoration outcomes actually produce undesirable communities and poor quality restorations early after restoration. These results focus on the short-term responses to spatial structure and may change over time. Our results illustrate that dynamics in real communities may be substantially different or more complex than those assumed in theoretical models and reveals the importance of testing ecological theory in the field.

In chapter 2 we incorporated tallgrass prairie restoration into existing management strategies to reduce Sericea abundance in heavily invaded land. For this experiment, we formulated restoration seed mixes with attributes thought to contribute to invasion resistance based upon predictions from invasion theory.  Our results show that methods used for site preparation affect the degree to which Sericea re-invades. Furthermore, densely sown seed mixes reduce Sericea invasion, but more diverse seed mixes do not. Similar to the first chapter, chapter 2 results inform restoration practice by demonstrating how ideas in ecological theory play out in realistic restoration settings.

In chapter 3, we sought to determine the relative importance of propagule pressure, disturbance, and invasion resistance in the distribution of Sericea invasion. We wanted to know if there are differences between the intrinsic invasion resistance of tallgrass prairie and abandoned cropland. We found that tallgrass prairie is intrinsically more resistant to invasion than abandoned cropland—an additional important ecosystem service that native prairie provides. We also showed that the landscape-scale distribution of Sericea is largely the result of human activity, the distribution of susceptible abandoned cropland, and the distance to established populations.

Multiple theoretical and practical themes emerged from the chapters in this dissertation. First, dominant species in tallgrass prairies heavily influence the composition of plant community by reducing the amount of fast growing species from the seed bank. In chapter 1, as aggregation declined and dominant species were distributed more widely, the abundance of seed bank weeds declined. This suppressive effect of dominant species seems to extend to Sericea. In chapter 2, experimental restorations sown more densely (where the majority of the seed mix consisted of dominant grass species) suppressed the re-invasion of Sericea from the seed bank more effectively than seed mixes with higher diversity. Our results from chapter 3 showed that the relatively high invasion resistance of tallgrass prairie affects Sericea's distribution at the landscape scale.

Second, spatial dynamics play an important role in dominant species abundance at local and landscape scales. At small scales, as in the Chapter 1 experiment, spatially restricting dominant species to local patches within the community reduced their abundance at the community scale, but when seeds are broadcasted over the entire restoration, dominant species are able to rapidly increase in abundance. At large scales we also saw that the spread of Sericea was facilitated by military activity, and at least part of this facilitation was due to the seed dispersal. In both cases, the extent to which dominant species (some desirable, one undesirable) became abundant in the community was affected by their seed dispersal. When the seeds of dominant species are aggregated at small or large scales, they likely experience intra-specific limitation. When left to their natural abilities to disperse, their abundance in the community is greatly restricted. If, on the other hand, seeds of dominant species are artificially augmented by humans, they quickly achieve high abundances and have the potential to exclude other species.

Third, there is no single best prairie community to use as a target for tallgrass prairie restoration. The community that is restored will be dependent upon the goals of the land manager; and the methods and seed mixes used for restoration should be altered accordingly. For example, if land managers primarily want to reduce the abundance of Sericea to maximize forage for livestock, seeding a dense stand of low diversity grasses followed by herbicide treatments may be an economic and effective strategy to minimize Sericea re-invasion. If diverse plant communities with high abundances of forb species are desired, it may be best to include a high amount of forb seed into the restoration seed mix and to avoid conducting such restorations on land invaded by Sericea. Dominant $C_4$ grasses are often viewed by restoration practitioners as a problematic group of species due to their aggressive nature. However, these species appear to be beneficial when attempting to limit the reestablishment of undesirable, aggressive species such as Sericea.

The chapters in this dissertation have shown that integrating ecological theory into restoration practice can both progress our understanding of ecological processes that regulate plant communities and also improve restoration outcomes. Restorations that become dominated by a few species and Sericea invasion are two of the most pressing issues for tallgrass prairie conservation. My hope is that these studies will provide valuable insight for restoration and conservation practitioners and also be an example of how ecological studies can be conducted in settings that are immediately relevant to practical restoration challenges.

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