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Effects of fine-scale plant arrangement on grassland establishment

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Effects of fine-scale plant arrangement on grassland establishment

by

Kathryn Anne Yurkonis

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

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ABSTRACT

Plants and their ramets often occur through space in non-random arrangements, potentially due to effects of local dispersal, competition with neighbors, and heterogeneity in the environment. Given that a plant's potential influence on others is limited in space, such plant pattern likely affects community dynamics. The studies presented further our understanding of effects of plant pattern by addressing if, and in what ways, fine-scale plant arrangement affects perennial grassland communities. In restored grasslands, I found that seeding method affected pattern formation, likely due to effects of altering local seed density and the depth at which seeds were sown. In these grasslands, fine-scale plant arrangement explained aspects of invader abundance that were not accounted for by plot-scale richness and evenness measures. In an experimental system, initial plant arrangement was related to subsequent invasion, but hypotheses concerning effects of arrangement on species coexistence were not supported. In total, these findings suggest that plant pattern may affect communities independently of the number and abundances of the species present and have implications for how practitioners might use knowledge of effects of initial plant arrangement to improve restoration success. Future studies will assess the mechanisms that underlie these responses and continue to investigate if restoration success may be improved by altering initial plant arrangement.

CHAPTER 1. GENERAL INTRODUCTION

Plant ecologists have long been interested in understanding why plants are arranged as they are within plant communities and whether or not such fine-scale arrangement, or pattern, will affect the ways a community will change in the future. Fine-scale plant pattern refers to the phenomenon in plant communities where individuals or ramets of the same species often occur together more than would be expected if they were randomly establishing through space (e.g. Glenn and Collins 1990, Bartha et al. 1995, Purves and Law 2002). Certainly abiotic factors broadly filter where individuals can and cannot establish, but it is less clear what factors control which individuals/ramets neighbor one another within a community, and if altering which individuals neighbor one another has consequences at larger scales. Given that a plant's potential influence on other plants is limited in space (Mack and Harper 1977, Casper et al. 2003, Vogt et al. 2010) and that a plant may perform differently if it is neighbored by conspecifics (individuals/ramets of the same species) or heterospecifics (individuals/ramets of different species) (Goldberg and Barton 1992, Rees et al. 1996, but see Milbau et al. 2007), such plant pattern likely affects community dynamics. Plant pattern may affect whether or not a community may be able to maintain present diversity levels into the future or be able to resist invasion by newly arriving species (Bergelson 1990, De Boeck et al. 2006). Thus, there is no shortage of studies addressing the causes and consequences of fine-scale spatial pattern in plant communities, but this link is challenging to address in an empirical way. The few empirical studies that have overcome the various limitations to studying pattern and process in communities suggest that pattern may affect diversity maintenance and invasion in plant communities (reviewed below), but much work needs to be done in this realm.

What causes plant pattern?

Plant pattern (non-random arrangement of conspecific ramets) may originate as a result of differences in seed/propagule arrangements as the community establishes, as a result of the ways species disperse through space once established, or as a result of individuals interacting with the biotic and abiotic environment (Kershaw 1963, Greig-Smith 1979). Although it seems that we should have a thorough understanding of how each of these factors contribute to the formation of plant pattern in communities, most studies have focused on quantifying pattern rather than elucidating which mechanisms contribute to the observed pattern.

Studies quantifying fine-scale pattern in plant communities burgeoned (e.g. Clark and Evans 1954, Kershaw 1958, 1959, Pielou 1962, Hill 1973b, Mack and Harper 1977, Greig-Smith 1979, citations within Purves and Law 2002) after publication of Watt's (1947) seminal paper on pattern and process in communities. These studies were mainly focused on describing pattern in plant communities and generally established that plants and their ramets are non-randomly arranged using a variety of metrics to describe pattern. For example, Kershaw (1958, 1959) assessed the spatial pattern of three species in an established English grassland community and concluded that pattern existed at several scales likely resulting from local dispersal, species interactions, and environmental heterogeneity. In a more recent study of plant pattern, De Luis et al. (2008) found that seedlings were conspecifically aggregated, i.e., occurred in clumps of conspecific individuals, after a fire in a Mediterranean grassland. These and many other studies have established that plants and their ramets are non-randomly arranged. However, it is often unclear what mechanisms contributed to the observed pattern.

A few studies have attempted to connect specific mechanisms to pattern formation, but the results have been mixed. Recently, several studies have altered local resource heterogeneity to determine if plant communities respond to fine-scale variation in the resource environment (Reynolds et al. 1997, Maestre et al. 2006, Reynolds et al. 2007). For example, in a restored grassland, total plant cover and aboveground biomass were more heterogeneous (had a higher coefficient of variation) when nutrients were supplied heterogeneously versus homogeneously, but diversity was lower due to proliferation of the dominant grass with nutrient enrichment (Baer et al. 2005). Total biomass production was also greater in communities containing *Lolium perenne* and/or *Plantago lanceolata* when nutrients were supplied heterogeneously in a phytotron study (Maestre et al. 2006). However, in an old-field system, biomass production was not affected by the arrangement of added soil nutrients (Reynolds et al. 2007). Often these types of studies only manipulate one resource at a time and it is difficult to separate effects of nutrient addition from *in situ* heterogeneity in nutrient supply. Furthermore, the scale of heterogeneity may be crucial in determining the community response and often only one scale of heterogeneity, which may or may not match the scales of *in situ* heterogeneity, is assessed.

Only a few studies have assessed influences of local dispersal, competitive effects, and environmental effects on plant pattern. Seabloom et al. (2005) compared model predictions of the effects of dispersal, competition, and heterogeneity on pattern formation in a California grassland with observed patterns. They found evidence suggesting that all three factors affected pattern formation in this system. Environmental heterogeneity was important in leading to aggregation within species early on and, in time, dispersal and competition led to segregation among species. Finally, in a rare experimental study, Moore (2009) assessed

patch formation in a single species (*Lupinus nanus*) in a California grassland. Moore (2009) found that changes in the size of *Lupinus* patches resulted from environmental and competitive effects and concluded that dispersal limitation was not a factor in the observed patch dynamics. Additional studies such as these are needed to characterize species scales of dispersal and competition to determine to what extent local dispersal, competition, and environmental heterogeneity affect pattern formation in plant communities.

How might plant pattern affect community dynamics?

Because effects of individuals on one another are limited in space, plant pattern may affect dynamics both of the resident species and newly establishing species. Theoretical studies have considered this question in various forms, but this has only been empirically demonstrated in a few cases. The most widely considered case is the effect of plant pattern on species coexistence. In classic Lotka-Volterra competition models, the only way for species to coexist is if individuals better withstand interactions with individuals of other species than with individuals of the same species. However, this assumes that plants disperse and compete globally, which may not be the case (Pacala 1997). Plants are restricted in the extent to which they disperse and compete with others (Mack and Harper 1977, Casper et al. 2003). When species coexistence models include such finite scales of interaction and information about where individuals are located, becoming more realistic than models that assume global dispersal and competition, interesting effects arise (reviewed in Pacala 1997, Tilman and Kareiva 1997, Silvertown and Wilson 2000, Amarasekare 2003, Bolker et al. 2003, Hoopes et al. 2005). In cases where species would otherwise exclude one another, species may coexist because they disperse or compete at different scales or respond to

environmental heterogeneity in different ways (Bolker et al. 2003, Snyder and Chesson 2004).

Elucidating the effects of such plant pattern on coexistence through empirical studies has been difficult because it is often difficult to manipulate pattern and it is often unclear at what scales individuals commonly interact (Casper et al. 2003, Murrell and Law 2003). However, a few studies have successfully tested effects of pattern on species coexistence. Stoll and Prati (2001) planted four annual species in random or intraspecifically aggregated patterns and found the planting arrangement affected species coexistence. Weaker competitors produced more biomass and stronger competitors produced less biomass when planted in the aggregated pattern. In a follow up study, Monzeglio and Stoll (2005) found weaker competitors had higher fitness in the aggregated patterns, but effects of plant arrangement on the stronger competitors was more complex. Norris et al. (2001b) also demonstrated that aggregating conspecific individuals affected fitness, but in this case reduced fitness of a common weed in tomato fields. Aggregating barnyard grass resulted in a 30-50% reduction in seed mass over random and regular arrangements at moderate densities (Norris et al. 2001b). More recently, Idjadi and Karlson (2007) and Hart and Marshall (2009) altered initial arrangement in corals and both found that some corals grew more when like individuals were grouped together. In low-richness systems, the initial arrangement of sessile organisms can affect the competitive environment that any given individual experiences, but it is unclear if such fine-scale pattern would affect larger-scale processes in more species-rich perennial communities with individuals arranged in more realistic patterns.

Fine-scale plant pattern may also affect invasion resistance by altering sites available for establishment by invading species. Establishment in a site is generally determined by the

density and identity of neighbors around the site (Fowler 1988, Bergelson et al. 1993, Herben et al. 2007, Milbau et al. 2007). Establishment is typically greater in sites surrounded by individuals of a few species than in sites surrounded by individuals of several different species because resources in these low-richness sites are not as completely consumed (Grubb 1977, Naeem et al. 2000, Loreau and Hector 2001, Kennedy et al. 2002). Altering plant pattern should affect the availability of such low-richness sites for invasion. Areas with individuals arranged into large, single species patches contain more low richness sites and, thus, may be less resistant to invasion than similar areas containing conspecific individuals arranged in several, smaller patches.

Although this could be an important consequence of plant pattern in perennial systems, only a few studies have considered effects of fine-scale plant pattern on invasion. Bergelson (1990) manipulated arrangements of individuals of *Poa annua* and found invasion by two annual weeds was higher when *P. annua* was planted in aggregated versus random patterns due to inhibition of invader establishment by litter. Bergelson et al. (1993) assessed effects of gap size and arrangement on invasion and found that a grassland invader spread more readily when available gaps for establishment were larger and closer together. Finally, Olsen et al. (2005) found that crop planting pattern affected weed recruitment, where weeds were less abundant when wheat was planted in a uniform pattern over rows. Although fine-scale plant pattern may affect invasion in species-rich perennial systems, this effect has not been investigated.

Quantifying plant pattern

One of the most difficult aspects of assessing causes and consequences of plant pattern in communities is manipulating and measuring plant pattern. The approaches that are available

to assess pattern can be broadly divided into those that quantify plant arrangement by mapping each individual/ramet or those that quantify plant arrangement based on occupancy in cells of a fine-scale map summarizing where plants are located in a community (Dale et al. 2002). Although recording the position of each individual is most desirable, as it provides information on local density and which individuals neighbor one another, this method is difficult to implement in perennial systems where it is nearly impossible to distinguish among genets and ramet density is often high. Throughout the studies presented here, pattern is assessed based on maps of the sampled communities and quantified based on metrics commonly used for assessing habitat pattern in landscape ecology (Riitters et al. 1995, Gardner and Urban 2007).

It is important to consider in what ways metrics describing plant pattern relate to metrics commonly used to describe community structure. Communities are commonly described through metrics that account for the number of species present and their relative abundances (Hill 1973a, Stirling and Wilsey 2001, Wilsey et al. 2005). Measures of plant arrangement may be linked to such richness and evenness measures, or measures of plant arrangement may explain more variation in community processes than richness/evenness measures. Changing species richness or evenness at coarse-scales (i.e., at the plot scale) affects the ways conspecific individuals/ramets associate with one another at finer-scales (De Boeck et al. 2006). Figure 1.1 demonstrates the relationship between coarse-scale richness and evenness and a variable describing mean patch size (the area occupied by a group of similarly shaded cells) in randomly generated communities. As coarse-scale richness or evenness increases the average area occupied by a group of similar cells decreases. Thus, when relating aspects of community dynamics (e.g., invasion resistance) to measures of

richness or evenness, we may be assessing the effects of adding a species or altering species abundances *and* effects of changing plant arrangement. Plant arrangement may also vary considerably at given richness/evenness levels within plant communities as a result of local dispersal and competition. Assessing the relationships among diversity measures and measures of plant pattern in naturally assembled communities would allow us to develop a clearer understanding of the effects of altering species richness and abundances in plant communities.

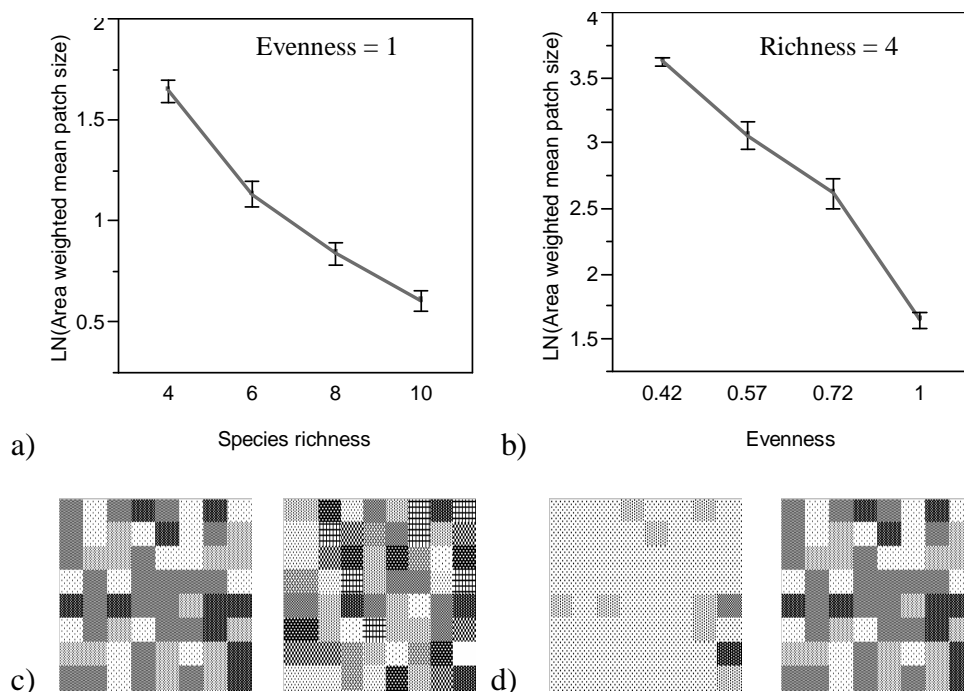


Figure 1.1 Hypothetical effects of changing plot-scale richness and evenness on fine-scale plant arrangement. The program QRULE was used to generate simple random maps each containing 64 individuals (one pixel = one individual) that either (a,c) varied in richness with constant evenness or (b,d) varied in evenness with constant richness. These were repeated at several richness and evenness levels $n = 10$ per richness/evenness combination. In restored prairies 3-11 species (mean = 7.3) were recorded per map with a mean map evenness of 0.45. c) Example of a map with species richness = 4 and 10 and constant evenness, d) Example of a map with evenness = 0.42 and 1 and constant richness. See Chapters 4 and 5 for more information on the area-weighted mean patch size variable.

Applications in restoration ecology

Investigating the factors that contribute to and the effects of fine-scale plant arrangement in grasslands has important applications in the field of restoration ecology. Throughout the tallgrass prairie region, sites once used for other purposes have been reconstructed into prairies starting with Aldo Leopold's first plantings at the University of Wisconsin Arboretum (Packard and Mutel 1997). Such tallgrass prairie restoration projects are planted in areas that range in size and for a variety of reasons ranging from purely aesthetic to restoring ecological function to the landscape (Packard and Mutel 1997, Wilson 2002). This is typically achieved by uniformly mixing seeds and planting them in a variety of ways. Despite our best efforts, plantings often contain large patches of conspecific ramets (Allison 2002, Derner et al. 2004, Yurkonis et al. In press-b). Furthermore, such restored plantings rarely resemble the remnant communities they are attempting to mimic (Allison 2002, Sluis 2002, Martin et al. 2005). Many factors may contribute to this outcome, ranging from the composition of the seed mix to the season of planting and subsequent disturbance at the site. These patches may also develop due to differences in competitive and dispersal abilities among the planted species (Tilman 1994, Bolker and Pacala 1999, Snyder and Chesson 2004), especially as some species are excluded by others during the first few years after planting (Wilson 2002). Understanding which factors contribute to this pattern formation may be helpful in improving restoration practices and advancing our basic understanding of the link between pattern and process in this often studied ecosystem (Bartha et al. 2004). In the future, practitioners might be able to improve their ability to restore ecosystems by manipulating the arrangement of sessile organisms at the start of a restoration project (Liu et al. 2004, Sleeman et al. 2005).

Dissertation Organization

In the following chapters, I investigate different aspects of the relationships between plant arrangement and community dynamics in tallgrass prairie plant communities. Chapters 2 and 3 ask if drill and broadcast seeding, two restoration techniques that differ in the ways seeds are incorporated into a restoration, produce plantings that differ in diversity, composition, and plant arrangement. Chapter 2 presents results from two sites each containing a drill and a broadcast seeded planting. The first was planted by J. Kooiker and the Story County Conservation Board and the second designed by A. van der Valk, D. Smith, and T. Rosburg. In Chapter 3, I present results from sampling replicated drill and broadcast plantings at Neal Smith National Wildlife Refuge in Prairie City, IA established by P. Drobney, D. L. Larson, and colleagues as part of a broader study of best restoration practices. In Chapter 4, I assess the relationships between richness, evenness, plant arrangement, and invasion in the Neal Smith study to determine if metrics describing plant arrangement explain some additional variation in invader abundance not captured by richness or evenness measures. In Chapter 5, I present the results from a study where I controlled plot scale richness and evenness while manipulating plant arrangement to assess if arrangement independently affects diversity and invasion in a grassland system. Each research chapter is presented as a paper for publication, which has either been modified from a paper in press (Chapters 2 and 3) or will be submitted shortly. Co-authors provided helpful suggestions for improvement at various stages for each project, but I remain responsible for the research and its presentation here and elsewhere. Finally, Chapter 6 provides general conclusions, implications for ecological restoration, and offers directions for future research. For brevity, all references are listed at the end of the dissertation in the literature cited section. Tables and figures are provided in text.

CHAPTER 2. THE IMPACT OF SEEDING METHOD ON DIVERSITY AND PLANT ARRANGEMENT IN TWO RESTORED GRASSLANDS

Modified from a paper to be published in *Restoration Ecology*

Kathryn A. Yurkonis, Brian J. Wilsey, Kirk A. Moloney and Arnold G. van der Valk

Abstract

Grassland restoration techniques are often compared based on the species richness and composition of the plantings they produce. Different techniques may also generate plantings that differ in the ways plants occupy space, an effect that is not often considered in the context of ecological restoration. This study tests if there are quadrat-scale (1 m²) differences between paired drill and broadcast seeded plantings in diversity, composition, and plant arrangement in two tallgrass prairie restoration sites. Higher competition intensity in and more contiguous spaces between rows in drill seeded restorations were hypothesized to result in larger patches of native warm-season grasses and non-native species than in broadcast seeded restorations. Drill and broadcast seeded plantings at both sites had similar Simpson's diversity and evenness. However, the effect of planting type on species richness, composition, and plant arrangement was site dependent. Native warm-season grasses in one site, and non-native species in the second, occupied more space and occurred in larger patches in drill seeded plantings. Furthermore, light at the soil surface was consistently lower in drill seeded plantings than in broadcast seeded plantings. This suggests that seed placement may affect the ways plants use space and resources in the resulting plantings. Future studies need to address if present differences between these planting types will result in future compositional differences and, if so, if altering seed patterns can meaningfully increase restoration success.

Introduction

Techniques used for grassland restoration may inadvertently influence the species richness and composition of the desired planting (Wilson 2002). Unfortunately, our understanding of the effects of various techniques on restoration success is quite limited, as their effects are rarely tested in controlled studies. Furthermore, although planting success is often judged against the richness and composition of the seed mix added to a site, we do not often consider if planting techniques affect the ways plants establish through space (Bartha et al. 2004). Such plant arrangement likely affects interactions among species and the composition of the planting because species dispersal and competition are inherently limited in their spatial extent (Bartha et al. 2004), but more studies of the effects of plant arrangement are needed. Considering grassland restorations may contain large single-species patches unlike their remnant counterparts (Allison 2002, Derner et al. 2004), developing our understanding of the effects planting techniques have on subsequent plant arrangement may help practitioners improve upon current restoration practices. This study provides a novel comparison of two common grassland restoration techniques by considering if they produce plantings that are similar in diversity, species composition, and fine-scale plant arrangement.

Drill and broadcast seeding are the two most common planting techniques used for restoring grasslands in the tallgrass prairie region. These methods differ in how seeds are planted in two ways. First, drill seeding places seeds deeper into the ground than broadcast seeding which places seeds on the soil surface. Because seeds that are planted deeper may have a higher germination rate (Redmann and Qi 1992, Ambrose and Wilson 2003), drill and broadcast seeded plantings may differ in species diversity and composition as a result of differences in the depth of seeding. Second, these techniques differ in the ways seeds are

arranged at planting. In drill seeded plantings, seeds are planted in equally spaced rows and the distances among neighboring seeds are rather short (Bufton 1978). In broadcast seeded plantings, seeds are generally spread across the landscape and distances between neighboring seeds are potentially longer than in a drill seeded planting, although local clumping may still occur. Of these methods, broadcasting may more closely mimic natural seed dispersal, which can be rather variable through space (Rabinowitz and Rapp 1980), but it is unclear if such seed position affects subsequent establishment.

As a result of differences in seed position at planting, seedlings in drill seeded plantings may experience more intense interactions with their neighbors than seedlings in broadcast seeded plantings. Establishing seedlings with closer neighbors may experience more initial negative interactions than those with further neighbors (Milbau et al. 2007). Early emerging species (Ross and Harper 1972) or strong competitors, which have a greater negative effect on other individuals than others have on it (Mack and Harper 1977), are most likely to benefit when distances between neighbors are relatively short. In the context of grassland restoration, these process may favor warm-season grasses which typically dominate plantings (Jackson 1999, Sluis 2002). This may lead to the creation of large, single species patches in drill seeded plantings as the strong competitors overtake adjacent weaker competitors and spread into unoccupied spaces between rows. Increased distances among strong and weak competitors in broadcast plantings may alleviate this effect of neighbor distance on establishment. Broadcast plantings may contain conspecific ramets arranged in smaller patches as weaker competitors are better able to establish.

Finally, when comparing drill and broadcast seeding it is important to consider if species establishment from the local propagule pool differs within these two types of

plantings. When planting into bare ground, the space available for weed establishment among sown seeds varies between the planting types and may affect invasion. In a single species experiment, weed recruitment was greater in plots with clumped versus random arrangements of *Poa annua* (Annual bluegrass) due to differences in local litter accumulation between treatments (Bergelson 1990). Non-native species invasion has also been shown to increase with gap size in central European meadows (Cascorbi 2007). These effects may translate into the occurrence of larger patches of weed species in drill seeded plantings.

Although drill and broadcast seeding are common, few studies have compared paired drill and broadcast seeded plantings to determine if they produce similar plantings and none have examined how plants establish in space in these two planting types. Bakker *et al.* (2003) found no differences in species establishment but higher survivorship when a mix of five grasses was broadcast into established non-native perennial grasses in a semi-arid system. Sheley *et al.* (2006) found greater density, but not biomass, of three perennial grasses drilled into pothole wetlands dominated by invasive species. Finally, Montalvo *et al.* (2002) found large seeded species had higher establishment when six species were drilled into coastal sage scrub. Although these results suggest that drill and broadcast seeding would generate different communities, it is unclear if plants occupy space in similar ways in the established plantings.

This study tests for differences in vegetation structure in paired drill and broadcast seeded tallgrass prairie plantings. We measured species diversity, composition, and fine-scale plant arrangement in two tallgrass prairie restorations. Within each site, the same seed mix was either drill or broadcast seeded into equal sized plantings. We test the hypotheses that in drill seeded plantings (1) species diversity would be lower, (2) native warm-season

grasses and non-native species would be more abundant, and (3) native warm-season grasses and non-native species would occur in larger patches. Although controlled experimental studies are still needed to directly test if the depth of seeding or seed arrangement contributes to structuring these communities, we determine if these planting techniques are interchangeable under realistic planting conditions.

Methods

Study Sites

A seven year old restoration (Peterson Park; Story County, Iowa, U.S.A.) and a four year old restoration (Lakeside Laboratory; Dickinson County, Iowa, U.S.A.) were sampled in June 2007. Both restorations occurred on land formerly in annual crop production and were located in the Des Moines Lobe landform region of Iowa. Each site contained a drill and a broadcast seeded planting. The drill and broadcast seeded areas were planted with the same seed mix and then managed in the same way within each site, but not across sites. These paired plantings provide an excellent opportunity to compare, with all other factors generally being equal, the differences between drill and broadcast seeded grassland restorations.

The Peterson Park site (lat 42° 05' N, long 93° 35' W) was planted in the fall of 1999 by the Story County Conservation Board. The site is located in the Skunk River floodplain and contains moderately to well drained Cumulic Hapludolls (DeWitt 1984). Mean annual temperature in the area is 8.8°C and mean annual precipitation is 837 mm. The site was divided into two sections, each planted with a seed mix containing 20 native species collected in bulk from three locations in Story County, Iowa. The northern 3.5 ha was planted at 15.6 kg pure live seed/ha with a broadcast seeder and cultipacked after seeding. The southern 1.9 ha was drill seeded with the same seed mix, mixed from the three sites in a

similar ratio, at 16.8 kg pure live seed/ha. The most abundant species within the bulk mix were *Solidago rigida* (Stiff goldenrod), *Ratibida pinnata* (Yellow coneflower), *Elymus canadensis* (Canada wildrye), *Andropogon gerardi* (Big bluestem), *Sorghastrum nutans* (Indian grass), and *Elymus virginicus* (Virginia wildrye). The entire site was burned in the springs of 2004, 2005, and 2006. The western half of the site was burned (½ of the drill seeded and ½ of the broadcast seeded planting) in the fall of 2006 and reseeded to increase species diversity (B. Gleason, Story County Conservation Board, Ames, IA, personal communication). As a result, sampling for this study was restricted to the eastern portion of the site.

The Lakeside Laboratory site (lat 43° 23' N, long 95° 10' W) is a 9.3 ha planting located on a south facing slope at the Iowa Lakeside Laboratory. Mean annual temperature in the area is 7.2°C and mean annual rainfall is 725 mm. Soils are predominantly Typic Hapludolls on 2-9% slope with some Cumulic Hapludolls (Dankert 1983). Soil series run East-West across the site and plantings were established with an equal proportion within each soil type (North-South). Sections (1.0 ha) that were drill or broadcast seeded with pure live seed during the spring of 2003 were sampled for this study. The site was disked twice and leveled with a cultipacker before planting. The entire site was drill seeded with the annual *Avena sativa* (Oat) as a cover crop (17.4 kg/ha) in the spring of 2002. A seed mix consisting of 37 forbs and 9 grasses was added at 12.0 kg pure live seed/ha within both plantings. The most abundant forbs (>10 seeds/m²) in the mixture were *Ratibida pinnata* (Yellow cone flower), *Rudbeckia hirta* (Black eyed susan), *Solidago rigida* (Stiff goldenrod), and *Petalostomum purpurea* (Purple prairie clover). The most abundant grasses were *Schizachyrium scoparium* (Little bluestem), *Koeleria macrantha* (Junegrass) and

Sorghastrum nutans (Indian grass). Both plantings have been mowed twice yearly (spring and late summer) to control thistles, primarily *Cirsium arvense* (Canada thistle) and *Carduus nutans* (Musk thistle).

Vegetation sampling

In each of the four plantings we sampled ten 1 m² quadrats. Quadrats were located randomly along and away from a transect through the longest portion of the planting. We used a 70 m transect at Peterson Park, and a 100 m transect at Lakeside Laboratory. All species were recorded and species composition was measured through point intercept sampling in each quadrat (Jonasson 1988, Frank and McNaughton 1990). A 1 m² sampling frame was placed over each plot and a pin dropped at 20 cm intervals in rows spaced 10 cm apart for a total of 40 pins/m². The identity of each leaf and stem touching the pin was recorded for each pin drop. Approximately 80% of the species in each plot were touched during sampling. To account for species that were not touched, a small value (0.5 hit) was added for each species with no hits when calculating diversity measures (Bowman et al. 2006). Species relative abundance was calculated by dividing the total touches for species *i* in a quadrat by the total touches in the quadrat. These data were used to determine species richness (*S*), Simpson's diversity ($1/D$), where $D = \sum p_i^2$ and p_i = relative abundance of species *i*, and evenness ($[1/D]/S$) at the quadrat-scale (Smith and Wilson 1996, Wilsey et al. 2005).

We used a cell-based approach (Herben et al. 1993) to map plant arrangement in each quadrat. Each 1 m² quadrat was divided into 64– 12.5 x 12.5 cm cells using metal rods passed through the vegetation. This cell size falls within the range of typical plant densities in a remnant tallgrass prairie (Losure et al. 2007) and was generally an appropriate scale for capturing individual plants. The species occupying 50% or more of the aboveground space

in the cell was recorded. This method generated a map of the species using the most resources and having the strongest influence throughout the quadrat. Although other metrics may better characterize pattern within this system (Glenn and Collins 1990, Bartha et al. 1995), we focus on patch-based metrics as an easily quantifiable indicator of local plant extent and, thus, potential species interaction and resource use patterns.

The program QRULE (Gardner 1999, Gardner and Urban 2007) was used to determine the number and size of single species patches within each quadrat. A patch was defined as a group of neighboring cells in the map of the quadrat dominated by the same species using an 8-neighbor rule (Turner et al. 2001). With this approach, the four cells immediately adjacent to and the four cells on the diagonal from a focal cell were considered neighboring cells. Two metrics were computed from these data: mean patch area (m^2), and patch mean-squared radius (m). Mean patch area values reflect the average size of areas dominated by continuous groups of ramets of the same species. The patch mean-squared radius metric, hereafter dispersion, is a measure of patch dispersion in meters (Gardner 1999). A larger area is needed to encompass an average patch in quadrats with larger dispersion values than in quadrats with smaller values (Gardner 1999). These metrics are generally uncorrelated, with the possible exception of patch size and dispersion (see Chapter 4) for maps with a large spatial extent and capture different aspects of spatial pattern within cell-based maps (Riitters et al. 1995, Gardner and Urban 2007).

We used two approaches to assess plant arrangement in the quadrats. The first analysis summarized plant arrangement by calculating the mean size and dispersion of *all* patches within the map of a quadrat, irrespective of the identity of the species that occupied each patch. A second analysis focused on how two groups of species, native warm-season

grasses and non-native species were collectively distributed within the map of each quadrat. Non-native species were defined as those that are introduced to North America. Both groups of species can dominate restorations despite efforts to promote realistic native species composition (Sluis 2002, Martin et al. 2005). For this analysis, each quadrat map was simplified into three classes: native warm-season grass, non-native species, and 'other'. Native warm-season and non-native species patches, which each could contain individuals from multiple species, were then summarized with QRULE. We calculated the proportion of the quadrat map covered by each species group and the mean size and dispersion of the heterospecific patches within each group. While the first analysis tests for differences in general patch structure, the second analysis tests if dominant species groups occupy space, and potentially utilize resources, within each planting in different ways.

Finally, photosynthetic active radiation (PAR) captured by the canopy was also measured as an estimate of resource use within each quadrat. A Decagon AccuPAR LP-80 sensor ceptometer (Pullman, Washington, U.S.A.) was used for the below canopy measurement with a Li-Cor external point sensor (Lincoln, Nebraska, U.S.A) for the above canopy measurement. Above and below canopy midday (10-2 CST) PAR was measured twice, in a North-South and East-West direction, within each quadrat and the results averaged. From the PAR data, we calculated the proportion of the available light that was captured by the canopy (1 minus proportion PAR at soil surface) as a proxy for overall resource capture in the quadrat.

Data analysis

We used analysis of variance (ANOVA; PROC GLM; SAS version 9.1) to test for quadrat-scale differences in species diversity, species composition, plant arrangement, and light

capture between drill and broadcast seeded plantings. Sown forb and non-native species relative abundance were arcsine squareroot transformed to meet normality assumptions. An initial ANOVA model included site, planting type, and site x planting type as fixed factors tested with the residual quadrat error term. With this analysis, we assess differences between plantings within these specific restorations. In most cases the interaction was significant and it was unreasonable to use the pooled error to test for model term significance. Therefore, we also present separate one-way ANOVA's for each site. A multi-response permutation procedure (MRPP; Zimmerman et al. 1985) based on a Bray – Curtis distance matrix (Vegan package in R; Oksanen et al. 2007) was performed to test for differences in species composition between plantings at each site. Finally, non-native plants at Peterson Park and native warm-season grasses at Lakeside Laboratory were not recorded as occupying cells in several quadrats and normality assumptions could not be met with data transformations for their arrangement metrics. A non-parametric Kruskal-Wallis test was performed to test for differences in plant arrangement metrics.

Results

Species Diversity

Although sites differed in some aspects of diversity, there was no main effect of planting type on quadrat-scale Simpson's Diversity, evenness, or species richness (Table 2.1; Fig. 2.1).

Because there was a site x planting type interaction for species richness (Table 2.1; Fig. 2.1), we also separately considered the effect of planting type on species richness within each site.

At Peterson Park, quadrat-scale species richness was similar between plantings ($F_{1,18} = 0.07$; $p > 0.05$), while quadrat-scale species richness was higher in the broadcast planting at Lakeside Laboratory ($F_{1,18} = 5.27$; $p = 0.03$).

Table 2.1 F-values from ANOVAs assessing the effects of drill and broadcast seeding on quadrat-scale richness (SR), Simpson's Diversity (1/D), and Evenness (E).

Source	df	SR	1/D	E	df	Pillai's Trace
Site (S)	1,36	87.84***	16.39***	1.14	3,34	28.10***
Planting type (P)	1,36	3.42	0.78	0.02	3,34	1.40
S x P	1,36	4.46*	1.58	0.16	3,34	1.69

* $p < 0.05$; *** $p < 0.001$

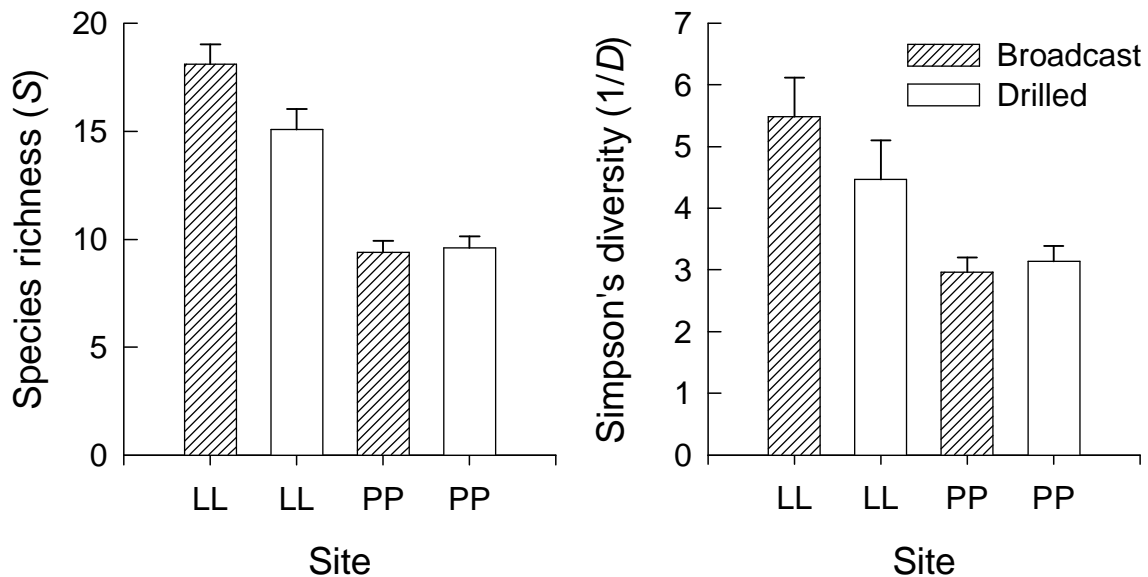


Figure 2.1 Species richness and Simpson's Diversity in drill and broadcast seeded plantings at Lakeside Laboratory (LL) and Peterson Park (PP). Means are shown \pm 1 SE from separate site ANOVA's.

Species composition

Of the species that established from the seed mix, the native warm-season grasses, *Andropogon gerardi*, *Sorghastrum nutans*, and *Schizachyrium scoparium* were most abundant (by number of point intercept touches) at both sites in addition to *Elymus canadensis* at Lakeside Laboratory. The most abundant non-native species at Peterson Park

were *Poa pratensis* and *Bromus inermis*. The most abundant non-native species at Lakeside Laboratory were *Bromus inermis*, *Poa pratensis*, *Elymus repens*, and *Dactylis glomerata*. Despite similarities in the species that occurred between sites, there were differences in the relative abundance of native warm-season grasses, sown forbs, and non-native species between sites (Table 2.2; Fig. 2.2). Peterson Park plantings were dominated by native warm-season grasses with few non-native species and Lakeside Laboratory plantings were dominated by non-native species with fewer native warm-season grasses (Fig. 2.2). There were also differences in the effect of planting type within each site (Table 2.2; Fig. 2.2). At Peterson Park there was no evidence of an effect of planting type on species composition (MRPP A = -0.004715; $p > 0.05$ for 1000 permutations). Native warm-season grasses ($F_{1,18} = 0.82$; $p > 0.05$; Fig. 2.2), sown forbs ($F_{1,18} = 0.08$; $p > 0.05$) and non-native species ($F_{1,18} = 0.25$, $p > 0.05$; Fig. 2.2) were similarly abundant between plantings. However, there was an effect of planting type on species composition at Lakeside Laboratory (MRPP A = 0.07654; $p < 0.01$ for 1000 permutations). Sown forb abundance ($F_{1,18} = 4.27$; $p < 0.10$) was similar between planting types. However, non-native species were more abundant ($F_{1,18} = 18.32$; $p < 0.001$) and native warm-season grasses less abundant ($F_{1,18} = 8.22$; $p < 0.05$) in the drill seeded planting than the broadcast seeded planting.

Table 2.2 F-values from ANOVAs assessing the effects of drill and broadcast seeding on species relative abundances.

Source	df	C4 grasses	Forbs	Non-native
Site (S)	1,36	116.92***	5.06*	93.05***
Planting type (P)	1,36	8.97**	2.60	17.24***
S x P	1,36	5.30*	3.63‡	14.25***

‡ $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

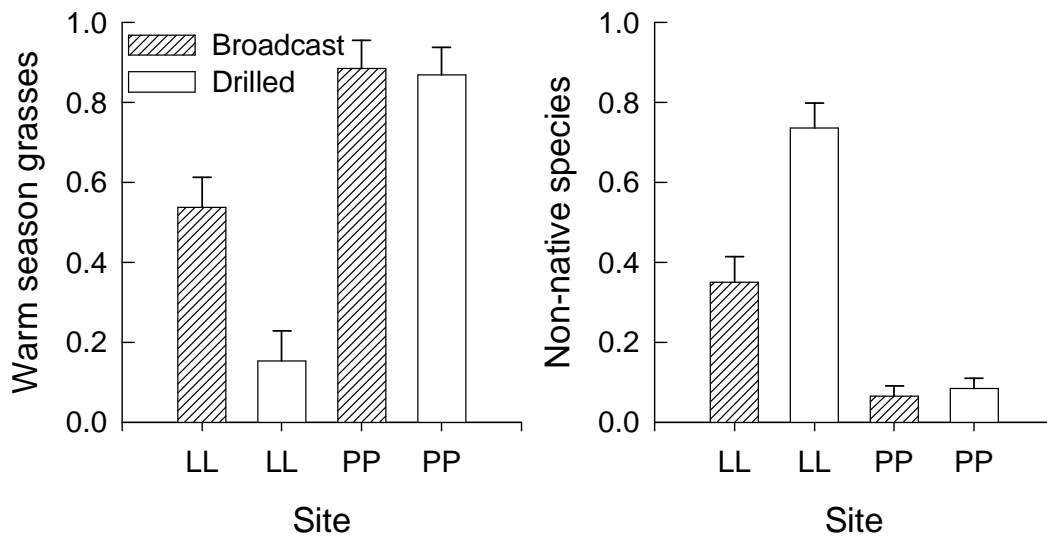


Figure 2.2 Species relative abundances in drill and broadcast seeded plantings at Lakeside Laboratory (LL) and Peterson Park (PP). Means are shown \pm 1 SE from separate site ANOVA's.

Plant arrangement

Mean patch size and dispersion per quadrat were similar between sites and planting types (Table 2.3; overall mean patch size = 0.0489 ± 0.00298 m², overall mean dispersion = 0.1779 ± 0.00199 m). However, groups of similar species established and were arranged differently between planting types. At Peterson Park, native warm-season (C₄) grasses were recorded in over half of the cells in both plantings. C₄ grasses occupied a larger proportion of cells per

Table 2.3 F-values from ANOVAs assessing the effects of drill and broadcast seeding on plant arrangement.

Source	df	Patch Size	Patch Dispersion	df	Pillai's Trace
Site (S)	1,36	0.22	4.11 [‡]	2,35	2.49 [‡]
Planting type (P)	1,36	3.73 [‡]	0.85	2,35	1.87
S x P	1,36	3.82 [‡]	3.06 [‡]	2,35	2.08

[‡] p < 0.10

quadrat ($F_{1,18} = 5.18$; $p = 0.0352$), and occurred in larger patches per quadrat ($F_{1,18} = 6.00$; $p = 0.0247$; Fig. 2.3) in the drill seeded than in the broadcast seeded planting. There was no effect of planting type on patch dispersion ($X^2 = 0.5714$; $df = 1$; $p > 0.05$; Fig. 2.3). Non-native species comprised a much lower proportion of space within quadrats at Peterson Park. Non-native species were recorded in four broadcast and one drill seeded quadrat at Peterson Park and there was no effect of planting type on non-native species proportion of space covered per quadrat ($X^2 = 2.2208$; $df = 1$; $p > 0.05$), mean patch size ($X^2 = 1.9371$; $df = 1$; $p > 0.05$, Fig. 2.3), or dispersion ($X^2 = 1.8054$; $df = 1$; $p > 0.05$, Fig. 2.3).

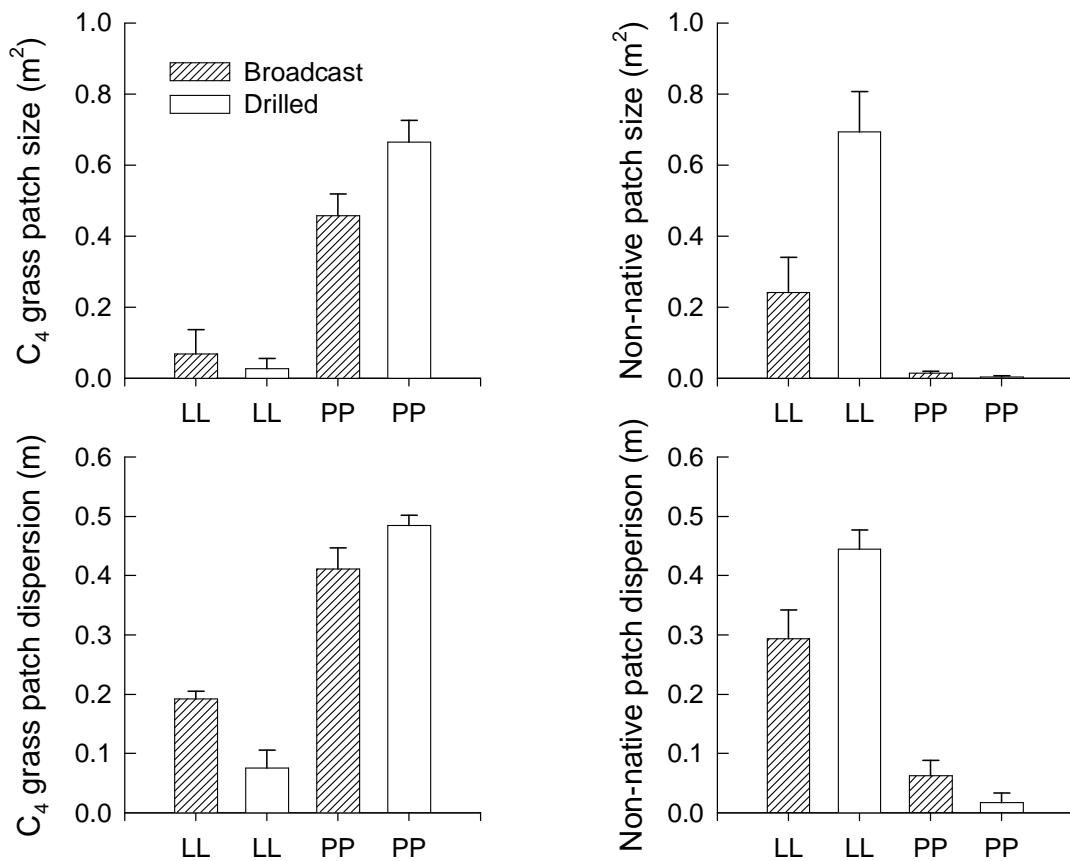


Figure 2.3 Native warm-season grass (C₄) and non-native plant arrangement in drill and broadcast seeded plantings at Lakeside Laboratory (LL) and Peterson Park (PP). Means are shown \pm 1 SE either from ANOVA or data depending on statistical test used.

At Lakeside Laboratory, these suites of species were arranged differently. Non-native species occupied greater proportion of cells, in some cases comprising the entire quadrat. In the drill seeded planting, non-native species occupied more cells ($F_{1,18} = 19.82$, $p = 0.0003$) and collectively occurred in larger ($X^2 = 8.6914$; $df = 1$; $p = 0.0032$, Fig. 2.3), similarly dispersed ($X^2 = 3.0400$; $df = 1$; $p = 0.0812$, Fig. 2.3) patches than in the broadcast planting. C_4 grasses were recorded in at least one cell in each broadcast quadrat and in four drill seeded quadrats. C_4 grasses occupied a larger proportion of space ($X^2 = 6.2325$; $df = 1$; $p = 0.0125$) and were more dispersed ($X^2 = 6.0142$; $df = 1$; $p = 0.0142$, Fig. 2.3) in broadcast quadrats but did not differ in patch size ($X^2 = 3.6708$; $df = 1$; $p > 0.05$, Fig. 2.3) between planting types.

Light Capture

Canopy light capture was similar between sites ($F_{1,36} = 1.16$, n.s.) but differed between planting types ($F_{1,36} = 16.92$, $p < 0.001$; planting type x site: $F_{1,36} = 0.44$, n.s.). Less light reached the soil surface in drill seeded quadrats (8.6 ± 1.7 %) than in broadcast quadrats (18.8 ± 1.7 %).

Discussion

This study tested whether vegetation structure differed between drill and broadcast seeded plantings in two established grassland restorations. Simpson's diversity and evenness at the quadrat-scale were similar between planting types in both sites. However, there were site-specific effects of planting type on species richness and composition. Species richness and composition were different between planting types in the site with a greater abundance of non-native species. A simple method used to quantify common plant arrangements revealed that the abundant species within each site were collectively distributed in larger patches in

drill seeded plantings. Finally, resource use, as measured by canopy light capture, was consistently greater in drill seeded plantings.

We expanded upon previous studies of drill and broadcast seeding by assessing if species richness and evenness components of plant diversity (Wilsey and Polley 2002, Ruiz-Jaen and Aide 2005), differ between planting types. Our hypothesis that diversity would be lower in drill seeded plantings, potentially due to greater competitive exclusion at establishment, was not supported. This result is consistent with comparisons between drill and broadcast seeded plantings in other systems. Studies in less species rich plantings (3-6 planted species, primarily perennial grasses) also found similar species richness between planting types (Montalvo et al. 2002, Sheley et al. 2006). These planting methods appear to be interchangeable when measuring restoration success through the lens of species diversity. However, these methods do not produce plantings that are similar in composition and plant arrangement.

The two sites differed in seed mix composition, timing of planting, and the ways each site were restored, including use of fire (Howe 1994) versus mowing (Williams et al. 2007). As a consequence, we analyzed each site independently for the effect of planting type. There was no effect of planting type on species composition at Peterson Park (fall seeded and burned), but there was in the more invaded Lakeside Laboratory (spring seeded and mowed) restoration. Native grass abundance was lower and non-native species abundance higher in the Lakeside Laboratory drill seeded planting. Although others suggest that drill seeding should facilitate native grass establishment (Jackson 1999), our findings are consistent with findings from Bakker *et al.* (2003) that broadcast seeding may increase native grass establishment under low invasion pressure. However, under greater invasion pressure,

drilling might lead to more non-sown species establishment than broadcast seeding (Bakker et al. 2003).

Native warm-season (C_4) grasses and non-native species occurred in larger patches in drill seeded plantings when they were abundant. Because richness was similar, this was likely not due to competitive exclusion leading to larger patch sizes as predicted. Rather, differences in arrangement likely resulted from individuals being placed more closely together and spreading through space differently between plantings. Although planting type did not affect C_4 grass abundance at Peterson Park, there was an effect of planting type on C_4 grass arrangements. C_4 grasses probably started more contiguously in drill seeded plantings because they were planted deeper, which may have increased their germination rate (Ambrose and Wilson 2003). As C_4 grasses established, they likely dictated what spaces could be occupied by other species (Glenn and Collins 1990).

We could not determine to what extent the planting method influenced invasion at Peterson Park because non-native species were so infrequent. However, results from Lakeside Laboratory suggest that planting method can influence invasion when there is greater invasion pressure. Non-native species were more abundant and occupied more space in drill seeded quadrats at Lakeside Laboratory. Non-native plants may have established more extensively in this drill seeded planting as a result of larger spaces for establishment (Bergelson et al. 1993). Further experiments are needed to test how the arrangement of gaps among establishing seedlings affects invasion in this setting.

We also found that canopy light capture was consistently higher in drill over broadcast seeded plantings. Within these sites, differences in light capture between plantings suggest that recruitment opportunities may become more limited in drill seeded plantings

than in broadcast plantings due to differences in microsites for establishment (Tilman 1997, Foster et al. 2007). As a result, we would predict higher species turnover in broadcast plantings due to increased light and more microsites for establishment (Foster et al. 2002, Foster et al. 2007). Differences in mean light capture and plant arrangement may also result in fine-scale differences in nutrient cycling (McKane et al. 1990, Foster et al. 2007) between these planting types.

Our results suggest planting methods can affect plant arrangement and resource use, without affecting diversity, which may have consequences for future vegetation dynamics via two mechanisms. Low neighborhood evenness resulting from the presence of large, conspecific patches may maintain future species diversity through the development of spatial refugia for weaker competitors (Stoll and Prati 2001, Monzeglio and Stoll 2005, Idjadi and Karlson 2007). In this scenario, species occurrence in *large* patches would be a desirable management objective. In contrast, low neighborhood evenness may destabilize diversity through higher invasibility (Tilman et al. 1996, Wilsey and Polley 2002). In this scenario, species occurrence in *small* patches would be a desirable management objective. The relative influence of each of these mechanisms needs further experimental testing to determine if seed arrangement at planting may be manipulated to maximize long-term maintenance of diversity in grassland restoration.

Incorporating a consideration of initial propagule arrangement in the restoration process has been important in wetland (Liu et al. 2004) and aquatic (Sleeman et al. 2005) systems and should be further considered in grassland restoration. The long-term effects of varying plant arrangements in space are especially important to consider when grasslands are being reconstructed in former agricultural lands (e.g. Muller et al. 1998, Walker et al. 2004)

where the seed bank has been depleted. This approach may also prove useful for understanding how other aspects of the soil biota (Viketoft 2007) and resources (Reynolds et al. 1997) develop in space.

This study is novel in that it takes a fine-scale approach to assessing grassland restoration success. We demonstrate that the arrangement of dominant species and resource capture differ among variously restored grasslands despite having similar levels of diversity. These differences may have long-term effects on vegetation dynamics. However, the mechanisms that generate plant arrangements and the implications of different arrangements for diversity maintenance and invasibility need to be further investigated. As we examine restorations to determine what aspects are and are not restorable (Hobbs 2007, Miller and Hobbs 2007), we need to consider how species utilize space and how plant pattern develops within plantings as a result of initial conditions and/or subsequent management (Bartha et al. 2004). By taking such a fine-scale approach to assessing and managing restorations we may be able to increase restoration success.

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**CHAPTER 3. SEEDING METHOD INFLUENCES WARM-SEASON GRASS
ABUNDANCE AND ARRANGEMENT BUT NOT LOCAL DIVERSITY IN
GRASSLAND RESTORATION**

Modified from a paper to be published in *Restoration Ecology*

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Pauline Drobney, and Diane L. Larson

Abstract

The arrangement of seedlings in newly restored communities may influence future species diversity and composition. We test the prediction that drill seeded grassland plantings would have lower species diversity, greater weed abundance, and conspecific ramets arranged in larger patches than otherwise similar broadcast seeded plantings. A diverse grassland seed mix was either drill seeded or broadcast seeded into 24 plots in each of three fields in 2005. In summer 2007, we measured species abundance in a 1 m² quadrat in each plot and mapped common species within the quadrat by recording the most abundant species in each of 64 cells. Quadrat-scale diversity and weed abundance were similar between drill and broadcast seeded plots, suggesting that processes that limited establishment and controlled invasion were not affected by these seeding methods. However, native warm-season (C₄) grasses were more abundant and occurred in less compact patches in drill seeded plots. This difference in C₄ grass abundance and arrangement may result from increased germination or vegetative propagation of C₄ grasses in drill seeded plots. Our findings suggest that local plant density may control fine-scale heterogeneity and species composition in restored grasslands, processes that need to be further investigated to determine if seed arrangements can be manipulated to increase diversity in restored grasslands.

Introduction

The initial arrangement of seeds in a planting may affect the ways newly established communities develop in time. This is an important aspect to consider when planning a restoration where several methods are available for incorporating seeds into a landscape (Wilson 2002). Seed arrangement may have unintentional and long lasting effects on restoration success (Allison 2002, Bartha et al. 2004) as a result of interactions that determine which species persist and their subsequent arrangement (Stoll and Prati 2001, Monzeglio and Stoll 2005, Korner et al. 2008). Although initial plant arrangement may affect species diversity and composition in established communities, studies have mostly considered this question in low-diversity, annual systems (e.g. Stoll and Prati 2001, Lortie et al. 2005, Monzeglio and Stoll 2005). Only a few studies (De Luis et al. 2008, Yurkonis et al. In press-b) have asked if initial plant arrangement is related to subsequent vegetation structure in species-rich perennial systems. Here, we ask if plant community structure, as measured by species diversity, composition, and fine-scale plant arrangement, differs between replicated drill and broadcast seeded grassland plots.

Drill and broadcast seeding methods differ in depth at which seeds are sown and the ways seeds are arranged at planting. These methods provide an interesting ecological context in which to study the effects initial plant arrangement may have on communities. In drill seeded restorations, seeds are planted in equally spaced rows with short distances between neighboring seeds and large, uniform spaces between rows (Bufton 1978). In broadcast seeded restorations, seeds are dispersed across the soil surface with potentially longer and more variable distances between neighboring seeds (Packard and Mutel 1997, Skinner 2005). Only a handful of studies have systematically compared these seeding techniques for

grassland restoration. Montalvo et al. (2002) found increased establishment of large seeded species in drill seeded coastal sage scrub and Sheley et al. (2006) found higher density of grasses in drill seeded pothole wetlands. In semi-arid grasslands, Bakker et al. (2003) found lower seedling survivorship in drill seeded plantings. These studies have been important in understanding potential effects of planting method on recruitment, but because they did not consider diversity and fine-scale heterogeneity we are unable to evaluate the long-term consequences of using either method.

There are several ways in which differences in planting method and subsequent seed arrangement may irreversibly affect plant community structure. Increased seeding depth (typically 1-2 cm) associated with drilling is predicted to favor grass germination (Redmann and Qi 1992). Initial seed arrangements may also affect species composition and diversity (richness and evenness) through interactions among neighbors. In establishing grasslands, survival of neighboring seedlings was most influenced by neighbors within a 3 cm distance (Milbau et al. 2007). Seedlings of strong competitors (Stoll and Prati 2001, Lortie et al. 2005, Vogt et al. 2010) or early emerging seedlings (Korner et al. 2008) are most likely to persist among such relatively close neighbors. If reducing neighbor distance lowers overall establishment and favors competitive dominants without affecting overall germination, then drill seeded plantings with shorter mean-nearest neighbor distances should be less diverse than otherwise similar broadcast seeded plantings.

Planting method may also affect how plants establish in space, a potentially important determinant of local resource uptake (De Boeck et al. 2006) and invasion resistance (Bergelson et al. 1993). Competitive exclusion of close neighbors may result in the formation of fewer, larger patches of conspecific individuals/ramets, whereas greater

distances among neighbors may result in more, smaller conspecific patches (Stoll and Prati 2001, Skinner 2005). If initial conditions dictate plant arrangement in this way, then drill seeded plantings with shorter nearest neighbor distances should contain conspecific ramets arranged in fewer, larger patches. Such differences in plant arrangement may then affect net resource uptake. When conspecific individuals/ramets are arranged in several small patches local resources may be more completely consumed, as richness will be greater at any given location, than when conspecifics are arranged in fewer, larger patches (Spehn et al. 2000, De Boeck et al. 2006). Investigating this effect of local density on plant arrangement in restorations would further our understanding of factors influencing formation of plant pattern and may provide insight into why restored sites are often less heterogeneous than reference sites (Allison 2002, Martin et al. 2005).

Finally, the seeding method used in a restoration may also affect recruitment from the local propagule pool. The arrangement of open space among establishing seedlings likely affects invasion by non-planted species (Goldberg and Werner 1983, Bergelson et al. 1993, Olsen et al. 2005). Larger, more contiguous open spaces, as in drill seeded plantings, may facilitate establishment from the local propagule pool over smaller, more dispersed spaces, as in broadcast plantings (Goldberg and Werner 1983, Bergelson et al. 1993, Milbau et al. 2007). In a single species experiment, weed recruitment was greater in plots with clumped versus random arrangements of *Poa annua* (Annual bluegrass) due to differences in local litter accumulation between treatments (Bergelson 1990). Invasion may also be affected by the ways in which resident species are arranged because larger, single species patches may not use resources as completely and are, thus, more susceptible to invasion (Tilman et al. 1996, Naeem et al. 2000). If the arrangement of open space and/or resident species affects

invasion then non-sown species should be more abundant in drill seeded plantings than in broadcast seeded plantings at comparable overall planting densities.

Drill and broadcast seeded grasslands may differ from one another as a result of initial differences in seeding depth, the proximity of nearest-neighbors, and the arrangement of available sites for establishment of non-seeded species. However, only a few studies have compared grasslands seeded with these methods to determine if such differences at seeding result in differences in the established restorations. A previous study (Chapter 2- Yurkonis et al. In press-b) in two separately managed tallgrass prairie reconstruction sites found that the relative abundance and arrangement of exotic species in one site and native warm-season grasses in a second site were greater in drill seeded plantings. Unfortunately, the sites in this study were not similarly managed, so it is difficult to determine if these methods produce consistently different plantings. This study expands upon our previous work by comparing vegetation structure in replicated drill and broadcast seeded plots to determine if there are consistent differences between these seeding methods.

We sampled replicated plots in a multi-field study to address the question: do drill and broadcast seeded grasslands differ in vegetation structure several years after planting? We test the hypotheses that in drill seeded plantings 1) species diversity will be lower, 2) weeds (native and exotic species not in the original seed mix) and native warm-season grasses will be more abundant, and 3) conspecific ramets of the sown species and ramets of native warm-season grasses in particular will be arranged in fewer, larger patches. Native warm-season grasses were of particular interest because they can dominate restorations despite efforts to promote realistic native species composition (Sluis 2002, Derner et al. 2004, Martin et al. 2005). Although controlled experimental studies are still needed to test

the mechanisms structuring these communities, such a comparative study allows us to quantify the net effects of drill and broadcast planting methods under realistic conditions.

Methods

Study Site

To assess the effects of drill and broadcast seeding on grassland restoration success experimental plots were planted in spring 2005 at Neal Smith National Wildlife Refuge (NSNWR; U.S. Fish and Wildlife Service, Prairie City, Iowa; lat 41° 33' N, long 93° 16' W). NSNWR is located on the southern Iowa drift plain where the mean annual temperature is 9.4°C and the mean annual precipitation is 836 mm. Three fields within the refuge were each planted with 24 replicate (12.2 x 12.2 m) plots that were either drill or broadcast seeded (2 seeding treatments x 12 replicates x 3 fields = 72 plots). All three fields, Production, Orbweaver, and Harmison, were in annual crop production the year before planting and were treated with herbicide (glyphosate and 2,4-D) prior to planting. Soils are relatively consistent within fields, but do vary among fields. The soils of the Production field are predominantly Aquertic Argiudolls, the soils of Orbweaver are mostly Oxyaquic Argiudolls, and the soils of Harmison are primarily Mollic Hapludalfs (Nestrud and Woster 1979). Production and Orbweaver soils formed in loess. Harmison soils formed in glacial till.

Plots were seeded (430 seeds/m²) with a 20 species seed mix (Table 3.1) where 70 percent of the seeds (by numbers) were grasses and 30 percent forbs, a ratio commonly used in large-scale plantings throughout the region (but not commonly used at NSNWR). Seeds were either drilled into the soil with a Tye seed drill (Lockney, Texas, U.S.A.; 20.32 cm spacing between rows) or broadcast over the soil surface with a Vicon broadcast seeder (Cotia, Brazil). The mix contained 13 forbs and seven grasses with *Elymus canadensis*

(Canada wildrye) seeded in a higher proportion (20%) than the remaining grasses (Table 3.1). Pure live seed was purchased from Allendan Seed Company in Winterset, IA and mixed onsite. All plots were mowed once in 2005 and 2006 and have not been burned.

Table 3.1 The number of quadrats (out of 24) containing each planted species in each field at NSNWR. HR = Harmison, OW = Orbweaver, and PP = Production.

Species ^a	Common name	HR	OW	PP
Grasses				
<i>Andropogon gerardii</i>	Big bluestem	20	21	22
<i>Bouteloua curtipendula</i>	Sideoats grama	21	17	15
<i>Elymus canadensis</i>	Canada wildrye	24	22	24
<i>Elymus virginicus</i> ^b	Virginia wildrye	1	1	-
<i>Panicum virgatum</i>	Switchgrass	12	13	16
<i>Sorghastrum nutans</i>	Indian grass	16	12	13
<i>Sporobolus asper</i>	Rough dropseed	5	7	1
<i>Schizachyrium scoparium</i>	Little bluestem	4	5	4
Legumes				
<i>Dalea candida</i>	White prairie clover	2	1	4
<i>Dalea purpurea</i>	Purple prairie clover	2	-	-
<i>Lespedeza capitata</i>	Round-headed bush clover	6	-	-
Forbs				
<i>Aster novae-angliae</i>	New England aster	22	7	7
<i>Chamaecrista fasciculata</i> ^b	Partridge pea	2	-	1
<i>Helianthus occidentalis</i>	Fewleaf sunflower	1	2	4
<i>Heliopsis helianthoides</i>	Smooth oxeye	2	2	6
<i>Monarda fistulosa</i>	Wild bergamot	1	6	8
<i>Rudbeckia hirta</i> ^b	Blackeyed Susan	6	4	3
<i>Echinacea pallida</i> ^b	Pale purple coneflower	-	1	-
<i>Solidago rigida</i>	Stiff goldenrod	1	1	1
<i>Solidago speciosa</i> ^b	Showy goldenrod	-	1	-
<i>Tradescantia ohiensis</i> ^b	Ohio spiderwort	-	-	1
<i>Verbena stricta</i>	Blue vervain	1	-	-
<i>Zizia aurea</i>	Golden Alexander	12	2	10

^a *Artemisia ludoviciana* (Prairie sage), *Coreopsis palmata* (Prairie coreopsis), and *Potentilla arguta* (Prairie cinquefoil) were in the seed mix, but were not present in the quadrats.

^b Species that were not included in the 20 species seed mix but were seeded elsewhere in the study.

Vegetation sampling

In July 2007 vegetation was sampled in a 1 m² quadrat randomly located to the north of the central marker in each plot (see Chapter 2 for additional details on the sampling method). Species were recorded and species composition measured through point intercept sampling (Jonasson 1988). To sample species composition, a 1 m² sampling frame was placed over each quadrat and 40 pins were positioned uniformly across the quadrat. The identity of every leaf and stem touched by each pin was recorded. A small value (0.5 touch) was added for each species that was present but was not touched by a pin when calculating diversity measures. Species relative abundance was calculated by dividing the total touches for species i in a quadrat by the total touches in the quadrat. These data were used to calculate planted species richness (S), Simpson's diversity ($1/D$), where $D = \sum p_i^2$ and p_i = relative abundance of species i , and evenness ($[1/D]/S$) at the quadrat-scale (Wilsey et al. 2005).

We used a cell based approach (Herben et al. 1993) to quantify plant arrangement in each quadrat. Each quadrat was divided into 64– 12.5 x 12.5 cm cells with metal rods passed through holes in the quadrat frame. This cell size falls within the range of typical plant densities in a remnant tallgrass prairie (Losure et al. 2007). We recorded the species that occupied 50% or more of the aboveground space in each cell. This method generated a fine-scale map of the species throughout the quadrat. The program QRULE (Gardner 1999, Gardner and Urban 2007) was used to analyze plant arrangement within each map. For each map we computed mean patch area (m²), and patch mean-squared radius (see Chapter 2 for descriptions). Patch mean-squared radius, hereafter dispersion, is a measure of within patch dispersion in meters, where larger values indicate that a larger area is needed to encompass a patch (Gardner 1999). A patch was defined as a group of neighboring cells (12.5 x 12.5 cm)

occupied by ramets of the same species where the four cells immediately adjacent to and the four cells on the diagonal from a focal cell were considered potential neighbors (Turner et al. 2001).

As in Yurkonis et al. (In press-b), we assessed plant arrangement in two ways. First, we calculated mean patch size and dispersion across *all* patches within the map of a quadrat, irrespective of the identity of the species recorded in each patch. Second, we calculated the proportion of the quadrat map covered by native warm-season (C_4) grasses and the mean size and dispersion of C_4 grass patches. For the C_4 grass analysis, each quadrat map was simplified into two classes, native warm-season grass and ‘other’, and then summarized via QRULE. Quadrats that did not include C_4 grasses were not included in analyses of C_4 grass arrangements, as seeds may not have been dispersed into these locations at planting. While the first analysis tested for differences in general plant arrangement, the second analysis tested if the dominant functional group in this system occupied space differently between plantings.

Photosynthetically active radiation (PAR) captured by the canopy was also measured within each quadrat with a Decagon AccuPAR LP-80 sensor light ceptometer (Pullman, Washington, U.S.A.) for the below canopy measurement and a Li-Cor external point sensor (Lincoln, Nebraska, U.S.A) for the above canopy measurement. Above and below canopy midday (10–2 CST) PAR was measured twice, in a North-South and East-West direction, within each quadrat and the results averaged. From the PAR data we calculated the proportion of available light captured (1 minus proportion PAR at soil surface) by the vegetation as a proxy for overall resource capture. We also calculated the variance to mean ratio, a measure of spatial heterogeneity (Dale et al. 2002), for each light reading (a series of

80 measurements) to test if differences occurred between planting types in the heterogeneity of light capture.

Data analysis

We used multivariate and univariate analysis of variance (MANOVA/ANOVA; PROC GLM; SAS Version 9.1; SAS Institute, Inc.) to test for quadrat-scale differences in planted species diversity, composition, plant arrangement, and light capture between drill and broadcast seeded quadrats. Multivariate tests were based on the Pillai's Trace test statistic and were used to test for overall effects among diversity and arrangement metrics. Species relative abundances were arcsine square root transformed and patch size and mean-squared radius data were log transformed to meet normality assumptions. Two quadrats (one drill and one broadcast) in Orbweaver were not included in the final analyses because they had no established planted species. We report type III sums of squares for the C₄ grass arrangement analysis because the number of drill and broadcast seeded quadrats containing C₄ grasses was unequal within each field. The analysis model included field, planting type and field x planting type as fixed factors tested with the residual quadrat error term. With this analysis, we assessed differences between plantings within these specific reconstructions.

Results

Although there were significant differences in the magnitude of some responses among fields, there were consistent treatment effects across fields and no significant treatment by field interactions for any of the analyses.

Planted species diversity

Individuals from 17 of the 20 species in the seed mix and from five species seeded elsewhere in the field were recorded in at least one of the quadrats. However, quadrat-scale diversity

did not reflect that of the seed mix. Only five species (all grasses) were consistently present in more than half of the quadrats (Table 3.1) and approximately one-quarter of the planted species were present in any given quadrat. Simpson's diversity, species richness, and evenness of the sown species were similar between planting types (Table 3.2; Fig. 3.1).

Simpson's diversity and evenness differed among fields and there was an overall effect of field on these diversity measures (Table 3.2; Fig. 3.1).

Table 3.2 F-values from a MANOVA assessing the effects of drill and broadcast seeding on Simpson's diversity (1/D), richness (SR), and evenness (E) at NSNWR.

Source	<i>df</i>	1/D	SR	E	<i>df</i>	Pillai's Trace
Field (F)	2,64	13.41***	1.61	8.54***	6,126	5.23***
Planting type (P)	1,64	3.24 [‡]	3.69 [‡]	0.08	3,62	2.31
F x P	2,64	0.30	0.04	0.11	6,126	0.13

[‡] $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

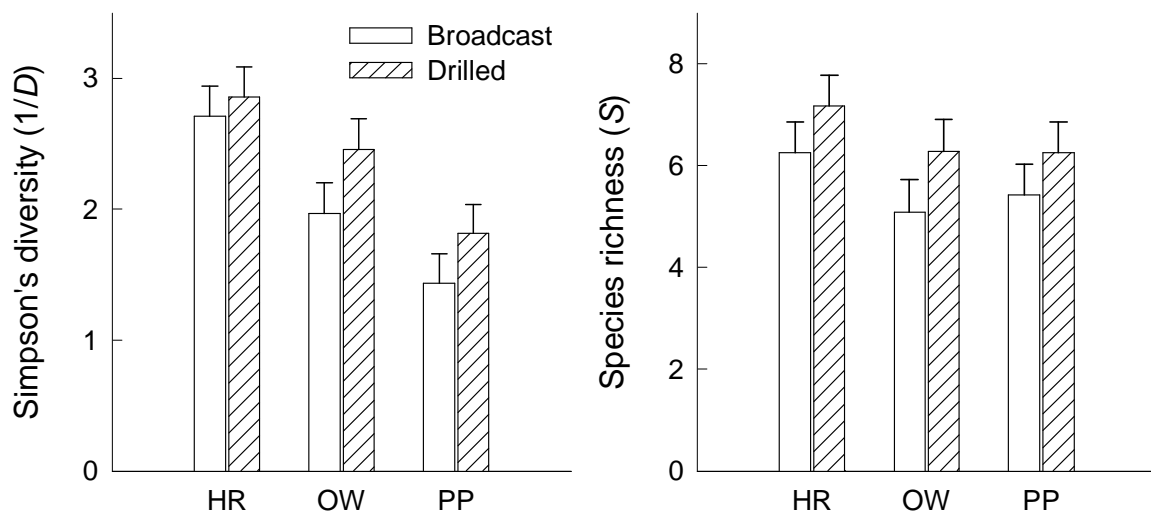


Figure 3.1 Simpson's diversity and richness in drill and broadcast seeded plantings at NSNWR. HR = Harmison, OW = Orbweaver, and PP = Production.

Species composition

Although planted species richness was low compared to that of the seed mix, over seventy-five percent of the leaf hits were from native planted species (Fig. 3.2). Quadrats were primarily comprised of *Elymus canadensis*. The most common non-sown species were the exotic *Setaria viridis* (Green bristlegrass) and the native *Conyza canadensis* (Canadian horseweed). Weed species abundance, the combined abundance of non-planted native species and exotic species, differed among fields ($F_{2,64} = 10.85$; $p < 0.001$), but was similar between planting types (Fig. 3.2; $F_{1,64} = 0.02$; $p > 0.05$; field x planting type, $F_{2,64} = 0.33$; $p > 0.05$). Native warm-season grasses, which included *Andropogon gerardii* (Big bluestem), *Panicum virgatum* (Switchgrass), *Schizachyrium scoparium* (Little bluestem), *Bouteloua curtipendula* (Sideoats grama), and *Sorghastrum nutans* (Indian grass), were equally abundant among fields ($F_{2,64} = 2.44$; $p = 0.10$) and more abundant in drill seeded quadrats (Fig. 3.2; $F_{2,64} = 4.58$; $p < 0.05$; field x planting type, $F_{2,64} = 0.53$; $p > 0.05$).

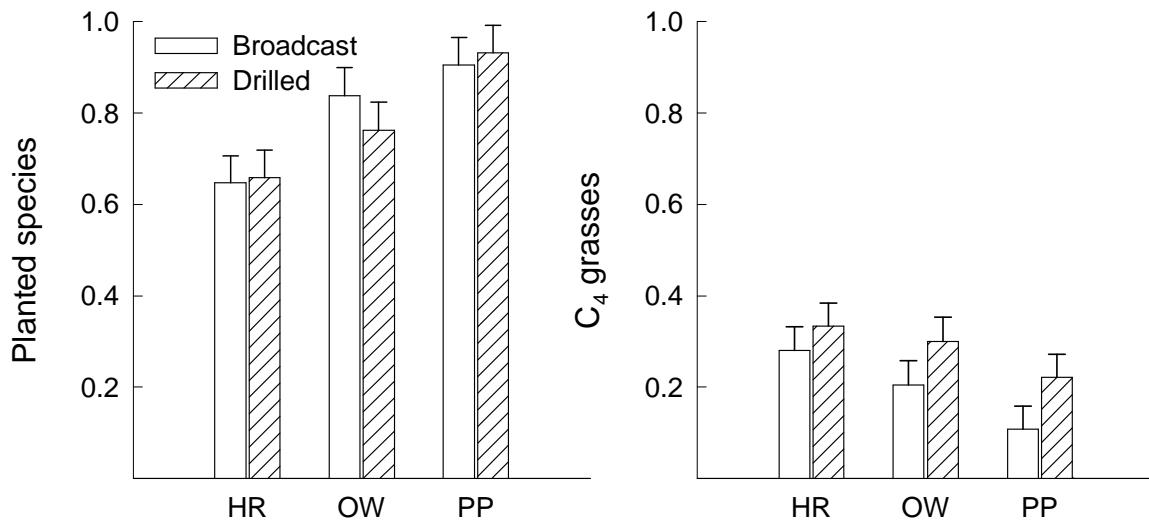


Figure 3.2 Species relative abundances in drill and broadcast seeded plantings at NSNWR. HR = Harmison, OW = Orbweaver, and PP = Production.

Plant arrangement

Mean patch size and dispersion differed among fields and were similar between planting types (Table 3.3, Fig. 3.3). Native warm-season grasses occupied space in different ways among fields and between drill and broadcast seeded quadrats (Table 3.4; Fig. 3.3).

Although there was no overall effect of planting type on warm-season grass arrangement, there were significant effects of planting type in the univariate tests. Drill seeded quadrats contained a greater proportion of C₄ grass attributed cells and more dispersed patches over broadcast seeded quadrats (Table 3.4; Fig. 3.3).

Table 3.3 F-values from a MANOVA assessing the effects of drill and broadcast seeding on plant arrangement metrics at NSNWR.

Source	<i>df</i>	Size	Dispersion	<i>df</i>	Pillai's Trace
Field (F)	2,64	25.25***	5.27**	4,128	10.64***
Planting type (P)	1,64	0.80	0.00	2,63	0.73
F x P	2,64	0.84	0.46	4,128	0.91

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

Table 3.4 F-values from a MANOVA assessing the effects of drill and broadcast seeding on C₄ grass arrangement metrics at NSNWR.

Source	<i>df</i>	Proportion	Size	Dispersion	<i>df</i>	Pillai's Trace
Field (F)	2,60	6.23**	4.70*	2.42 [‡]	6,118	2.29*
Planting type (P)	1,60	4.39*	3.15 [‡]	4.27*	3,58	1.69
F x P	2,60	0.12	0.0016	0.28	6,118	0.61

[‡] $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

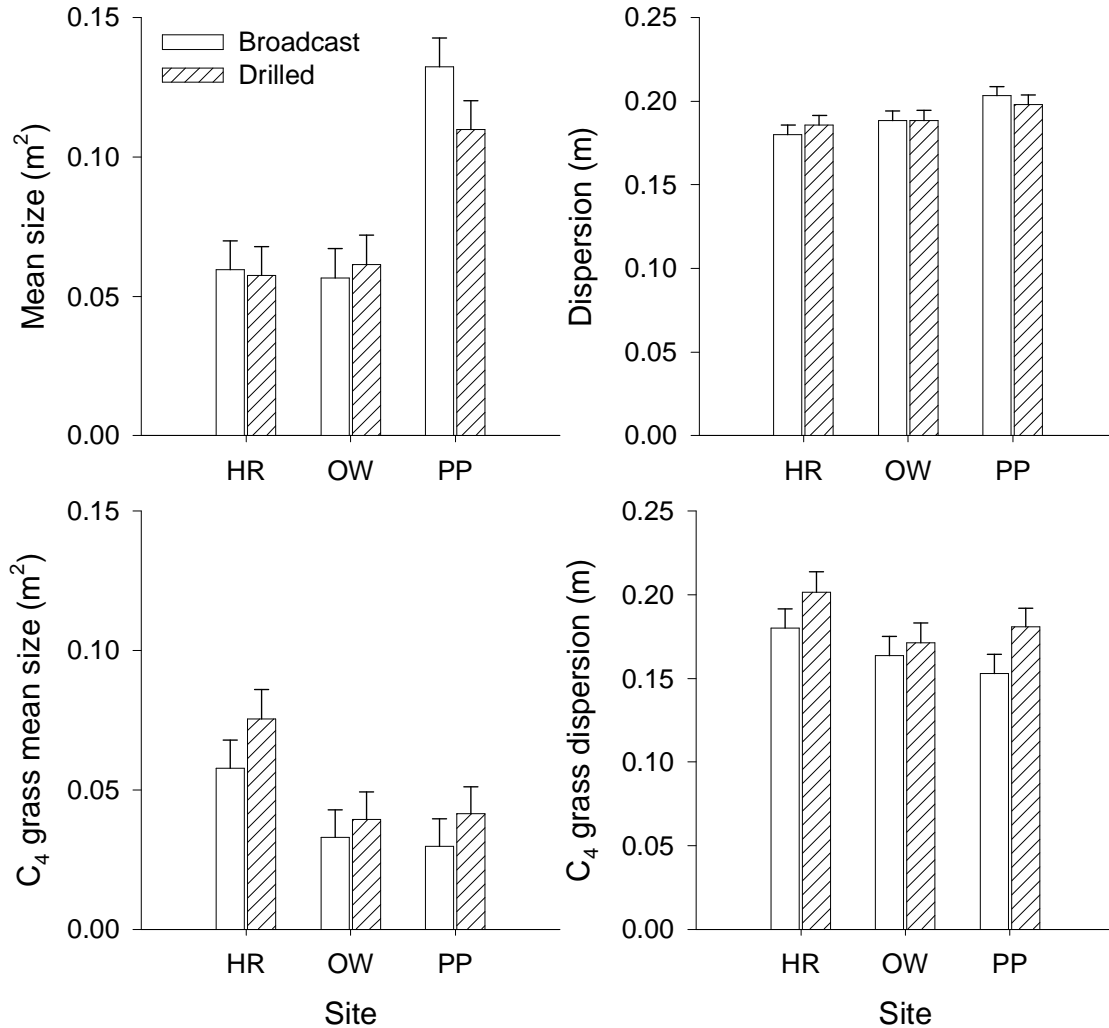


Figure 3.3 Arrangement of all species and C₄ grasses in drill and broadcast seeded plantings at NSNWR. HR = Harmison, OW = Orbweaver, and PP = Production.

Resource use

Mean light uptake was similar between planting types ($F_{1,64} = 2.65$, $p > 0.05$) and among fields ($F_{2,64} = 2.94$, $p > 0.05$; field x planting type: $F_{2,64} = 0.04$, $p > 0.05$; mean = 0.81 ± 0.013). In addition, the variance to mean ratio of the light measurements was similar between treatments ($F_{1,64} = 0.14$, $p > 0.05$) but not among fields ($F_{2,64} = 3.17$, $p < 0.05$; field

x planting type: $F_{2,64} = 0.06$, $p > 0.05$; Harmison = 0.127 ± 0.008 ; Orbweaver = 0.108 ± 0.008 ; Production = 0.140 ± 0.010).

Discussion

We compared drill and broadcast seeded grassland plots, which varied in the depth to which seeds were sown and in the arrangement of seeds at planting, to determine if initial planting method influences grassland establishment. As in Yurkonis et al. (In press-b), we found that planting method did not affect quadrat-scale Simpson's diversity, species richness, or evenness in these plantings. We also found that weed relative abundance was similar between quadrats in drill and broadcast seeded plots. These results suggest that the processes regulating species establishment and invasion were not affected by altering the seeding methods, and we conclude that, from a management perspective, drill and broadcast seeding are interchangeable in this regard.

Interactions should be more intense among closer individuals in establishing communities (Vogt et al. 2010), such that communities that differ in initial seed arrangement (local density) should differ in composition and diversity. However, our findings suggest that altering local seed density while maintaining coarser-scale density did not affect overall species establishment and subsequent diversity. There are several potential causes for this outcome. The effects of arranging seeds into rows in drill seeded plots may have been offset by seed movement along the ground surface after planting (Harper et al. 1965) or seedlings growing into the large open spaces between rows (Coulson et al. 2001). Seed density may also have been low enough that seeds were placed far enough apart as not to be influenced by establishing neighbors (Milbau et al. 2007) in both treatments, although 430 seeds/m^2 is greater than most recommended seeding densities (Packard and Mutel 1997, Wilson 2002).

Finally, germination may have been higher in drill seeded plots, which could have offset negative effects of local density in drill seeded plots. In a separate greenhouse study, seedling density was greater in simulated drill seeded plantings than in simulated broadcast seeded plantings seeded at 3940 seeds/m² (Yurkonis, unpublished data), likely due to increased germination with greater seeding depth (Redmann and Qi 1992). This difference persisted to the end of the first growing season as the number of individuals declined due to thinning. More seedlings were competitively excluded in the drill seeded treatment, but the outcome of thinning was similar between treatments. Species diversity, richness, and evenness were similar between drill and broadcast seeded treatments at the end of the study (Yurkonis, unpublished data). In the present study, thinning may also have affected species equally between realistic drill and broadcast seeded plantings. Unfortunately, we were unable to measure seedling density at the start of the experiment, so we leave future studies to test among these scenarios of seedling interactions.

Generally, species establishment from the seed mix was low in both types of plots. We used a seed mix with a high proportion of grasses which may have out competed forb seedlings in the establishing plantings (Dickson and Busby 2009). However, increasing the percentage of forbs did not result in an increase in species richness in an additional seeding treatment in this study (Larson, unpublished data). Other factors that could affect species establishment equally between planting types include season of planting (fall versus spring) and seed predation (Packard and Mutel 1997, Wilson 2002). Future studies need to control for such factors that limit overall establishment to test the role that changing distances among neighboring seeds, while maintaining overall density, plays in establishing grasslands.

Exotic species and native non-planted species were predicted to establish more frequently in the larger and more contiguous open spaces (Bergelson 1990, Bergelson et al. 1993) between rows in drill seeded plots. However, in this site there were no differences in weed abundance between drill and broadcast seeded plots. Thus far, previous studies have found mixed effects of drill versus broadcast seeding on species invasion. Sheley et al. (2006) found no effect of planting method on weed abundance when perennial grasses were drill and broadcast seeded into pothole wetlands. However, the introduced grass *Agropyron cristatum* (Crested wheatgrass) was occasionally more abundant when native species were drill seeded than when they were broadcast seeded into semi-arid grasslands dominated by the grass (Bakker et al. 2003). Exotic species were more abundant in a drill seeded planting at a second site in the tallgrass prairie region and were similar in abundance between a drill and broadcast seeded planting in yet a third location under a different management regime (Yurkonis et al. in press). Differences among sites in the response of weed species to these planting methods may be attributable to differences in the size of the weed seed bank. Prior agricultural production in these fields likely reduced the weed seed bank to a few annual invaders (Menalled et al. 2001), which may have been quickly out-competed by establishing perennials. In grasslands reconstructed in former agriculture fields, invaders may become more problematic over time (Naeem et al. 2000, De Cauwer et al. 2005).

Although other aspects of plant community structure were similar between seeding treatments, the dominant species in this system, native warm-season grasses, responded differently to drill and broadcast seeding. C₄ grasses were more abundant and occurred in less compact patches in drill seeded plots. The C₄ grasses were not present prior to planting due to the long history of annual crop production in these fields and had to have established

from seed. Germination and resulting abundance may have been higher in drill seeded plots as a result of increased seeding depth (1 cm versus surface seeding in broadcast plots) (Redmann & Qi 1992). Differences in arrangement may result from the aggregation of seeds during the drilling process, fine-scale seed movement due to differences in ground surface topography with drilling (Harper et al. 1965; Bufton 1978), or differences in vegetative propagation into unoccupied areas (Packard & Mutel 1997). Local microsites (e.g., soil characteristics) can also control establishment, but we would expect the same patterns between drill and broadcast seeded plots. Our findings support other non-spatial studies of drill and broadcast seeded plantings which have found higher survivorship (Bakker et al. 2003), biomass (Jackson 1999), and density (Sheley et al. 2006) of native grasses in drill seeded plantings.

Over time, C₄ grass abundance may increase in these plots (Sluis 2002, Derner et al. 2004) and their present arrangements may have long-term effects on local species turnover. C₄ grasses are maintained by vegetative propagation and fragmentation and can persist for multiple decades (Derner et al. 2004), although some species may be much more dynamic over shorter time scales (Herben et al. 1993). Because the dominant plants may be relatively stable in their positions through time, it is important to consider how their arrangement early in a restoration may affect local resource use and future species turnover. Benson and Hartnett (2006) found that in a remnant grassland, most new individuals arise from vegetative recruitment from long-lived individuals as opposed to seedling establishment. Seedling recruitment is also likely limited in established grassland restorations, but further work is needed to investigate this question.

The arrangement of dominant long-lived individuals, such as C₄ grasses, may affect rates of competitive exclusion, resource use, and species turnover (Tilman 1993; De Boeck et al. 2006; Racz & Karsai 2006) in communities. C₄ grasses consume nutrients differently than C₃ grasses and forbs (Wedin and Tilman 1990). Thus, dispersed patches of C₄ grasses may affect local resource cycling more extensively than compact patches (Spehn et al. 2000; De Boeck et al. 2006). Differences in resource uptake associated with different plant arrangements may then affect resources available for local colonization and alter invasibility and species turnover (Tilman 1993, Naeem et al. 2000). Although there were no differences in light use, a proxy for resource use, among these fields, similar older plantings did have differences in light uptake between drill and broadcast seeded plantings (Yurkonis et al. In press-b). Further testing is needed to determine if plant arrangements in established communities have long-term effects on community dynamics.

Conclusions

By considering species diversity and fine-scale plant arrangement in planning and assessing restorations, we can further our understanding of the mechanisms controlling community assembly in restored and natural systems. This application of spatial theory in restoration practice has been proposed for restoration of wild rice marshes (Liu et al. 2004), coral reefs (Sleeman et al. 2005), and plant communities in general (Bartha et al. 2004). Previous studies have shown that neighbor associations are important for determining local colonization (Goldberg & Werner 1983; Milbau et al. 2007) and extinction (Stoll & Prati 2001) and that spatially dependent processes may be important for determining long-term community dynamics (reviewed in Tilman and Kareiva 1997). Our findings suggest that local plant density may control fine-scale heterogeneity in restored grasslands and demonstrate

that plant arrangement is a potentially important factor to consider when initiating a restoration in sites that have been previously depleted of their native species pool (e.g. Muller et al. 1998, Walker et al. 2004). These methods need to be further investigated to determine if local density affects long-term resource use and diversity maintenance in these plantings and if fine-scale plant arrangement may be manipulated in other ways (e.g., by arranging individuals with the same identity together) to increase diversity in restored communities.

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CHAPTER 4. NATIVE PLANT RICHNESS, EVENNESS, AND ARRANGEMENT AS PREDICTORS OF GRASSLAND INVADER ABUNDANCE

A paper to be submitted to *Oikos*

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Abstract

Species richness and evenness components of plant species diversity account for the number and relative abundance of species in a given locale and are related to local invasion. However, these metrics may not account for the ways that resident species occupy space, which may also dictate local invasion. We used species composition and plant arrangement data collected from 1 m² quadrats in a grassland reconstruction study to assess the relationships among sown species richness, evenness, and plant arrangement and if they relate to invader abundance in a given growing season. Arrangement metrics were independent in one field and dependent on species richness and evenness in the remaining fields. Path analysis was used to confirm a theoretical model linking diversity and arrangement metrics with invader abundance. Evenness and invader abundance were not directly related. However, sown species richness and mean patch size were consistently inversely related to one another and to invader abundance. Quadrats with lower species richness and larger patches were less invaded, likely an effect of the dominant species *Elymus canadensis* inhibiting establishment of cool season invaders. Our results suggest that species richness and evenness may not account for the ways species occupy space and that plant arrangement may independently relate to invasion. Approaching diversity-invasion relationships with this framework will allow future studies to separate effects of species diversity attributable to plant arrangement from effects attributable to the presence of

multiple species in a locale and may reconcile inconsistencies among diversity-invasion studies.

Introduction

Diversity – invasion studies commonly relate invader abundance to the number (richness) and abundances (evenness) of resident species at the plot-scale (e.g., Wilsey and Polley 2002, Emery and Gross 2007, Mattingly et al. 2007). However, these metrics may not account for finer-scale heterogeneity. Conspecific ramets are often aggregated at fine scales (Thorhallsdottir 1990, Herben et al. 1993, Bartha et al. 1995) due to effects of localized dispersal and competition and species responses to local resource heterogeneity (Snyder and Chesson 2004, Seabloom et al. 2005). Since the effect of any individual on establishment is potentially restricted in space, such arrangement may affect invasion independently of plot-scale richness and evenness. Including measures of plant arrangement in diversity-invasion studies may explain additional variation in invader abundance and would provide an avenue for separating effects of species composition from effects of fine-scale heterogeneity on plot-scale invasion (Grace 1999).

Whether or not a new individual establishes successfully is determined by the conditions at the potential establishment site, which may be affected by immediate or more distant neighbors. The neighbors immediately adjacent to a potential establishment site most strongly affect focal plant performance as they are presumed to exert the greatest control over local resource availability (Goldberg 1987, Naeem et al. 2000, Kennedy et al. 2002, Milbau et al. 2005, Herben et al. 2007, Milbau et al. 2007). Kennedy et al. (2002) studied the effect of species richness and density within a 10 cm radius of an invader on grassland invasion and found that invaders performed better in less species rich and less crowded neighborhoods.

Milbau et al (2007) studied the effects of several neighborhood characteristics on establishment of grassland invaders and found that invader performance was most strongly determined by the number of neighbors in a 3 cm neighborhood and light availability when the neighborhood size was extended to 8 cm. Distant plants may also affect invasion by forming an extensive canopy/root structure or through diffuse soil feedbacks, but their effects are expected to rapidly decline with distance from their rooted location and need further investigation (Bever 2003, Casper et al. 2003).

If the effects of an individual on invasion are restricted in space to a scale finer than the plot scale, metrics describing the arrangement of conspecific individuals may more effectively explain plot-scale invasion than plot-scale species richness or evenness. Because invasion is more likely to be successful in locations where resident individuals do not completely consume local resources (Kennedy et al. 2002, Milbau et al. 2005) neighborhoods dominated by a single species are more likely to be invaded than neighborhoods consisting of several species. In this way finer-scale heterogeneity in a plot may have an effect on local invasion that is independent of the identity or abundances of the species in a plot. If conspecific individuals/ramets are grouped together in a plot (occurring in large patches) then there should be more low richness/low evenness neighborhoods and more available locations for establishment than if the same individuals/ramets were spread through a plot (occurring in smaller patches) where more species are likely to interact at potential establishment sites.

Although several studies have characterized neighborhood effects on invasion (Naeem et al. 2000, Kennedy et al. 2002, Milbau et al. 2007), only a few studies have quantified the effects of fine-scale plant arrangement on plot-scale invasion. Bergelson (1990) manipulated arrangement of *Poa annua* individuals and found invasion by two annual

weeds was higher when *P. annua* was planted in aggregated versus random arrays due to inhibition of invader establishment by litter. However, this study was limited to assessing the effects of heterogeneity within a single species on invasion. In a study of the effects of initial plant arrangement of multiple grassland species on invasion we found invader abundance at the plot-scale was greater in plots containing conspecific individuals arranged in fewer, larger patches (Chapter 5). Unfortunately, these studies do not assess the relative influences of species richness, evenness, and arrangement on invasion, so it is unclear which parameters most strongly correlate with invader abundance.

By simultaneously assessing the relationships between species richness, evenness, plant arrangement, and invader abundance we can determine if heterogeneity explains some additional aspect of invasion resistance that is not accounted for by richness and evenness measures alone. To some extent, fine-scale plant arrangement is restricted by plot-scale species richness and evenness, and effects of arrangement may therefore be explained by these metrics. As species richness declines the area available for each species increases (De Boeck et al. 2006). If species relative abundance is correlated with the proportion of the ground surface covered by a species, as evenness declines the area available for each species also increases. Thus evenness and richness measures, which are typically independent of one another (Wilsey et al. 2005) may be negatively related to plant arrangement metrics. If richness and evenness describe plant arrangement, the effects of richness and evenness on invasion resistance could be separated into two components: a direct effect and an indirect effect attributable to the effects of arrangement on invasion (Figure 4.1).

To evaluate the relationships among species richness, evenness, plant arrangement, and invader abundance, we used multivariate statistics to test for direct and indirect

relationships among these metrics in reconstructed grassland plots. Path analysis was used to assess a theoretical model linking these metrics and determine the direct and indirect effects of species richness, evenness, and arrangement on invasion (Figure 4.1). Because we are interested in determining if arrangement metrics are dependent on richness and evenness, this study focuses on arrangement as constrained by species richness and evenness or as an independent descriptor of invasion. We address the questions: 1) Are species richness, evenness, and arrangement empirically independent at plot-scales? and 2) Which of these aspects of community structure are correlated with invader abundance in experimental grassland plots? This study provides a novel assessment of the relationships among species arrangement, richness and evenness and their relationships with invasion at the plot scale. By testing effects of diversity versus effects of fine-scale heterogeneity on invasion within this framework we can begin to understand what role local heterogeneity plays in invasion resistance.

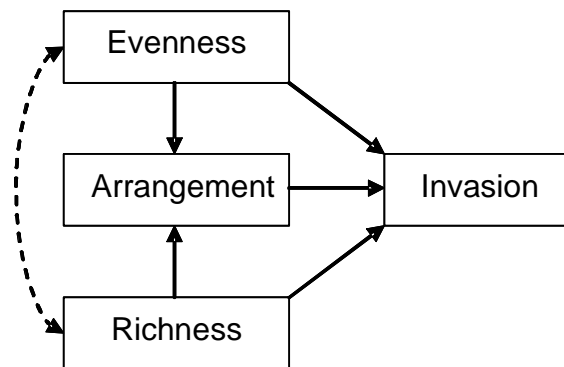


Figure 4.1 Proposed relationships among metrics describing vegetation structure and their effects on invasion. The dashed line indicates that we expect a non-significant correlation between species richness and evenness. Plant arrangement may affect invasion independently of effects attributable to species richness and evenness.

Methods

Study site

In July 2007, spring planted (2005) grassland plots were sampled at Neal Smith National Wildlife Refuge (NSNWR, U.S. Fish and Wildlife Service, Prairie City, IA U.S.A.). The mean annual temperature at the site is 9.4°C and, on average, the site receives 836 mm of precipitation a year. We sampled plots (12.2 x 12.2 m) that were planted via drill seeding or broadcast seeding in three fields (3 fields x 2 planting types x 12 replicates = 72 plots). Plots were seeded (430 seeds m⁻²) with a 20 species seed mix, where 70 percent of the seeds (by numbers) were grasses (7 species) and 30 percent forbs (13 species). *Elymus canadensis* L. (Canada wild rye) was seeded in a higher proportion than the remaining grasses (20% vs. 15% for *Andropogon gerardii* and 7% for the others). The seed mix was either drilled into the ground with a Tye seed drill (Lockney, TX, U.S.A.; 20.32 cm spacing between rows) or broadcast over the ground surface with a Vicon broadcast seeder (Cotia, Brazil). All plots were mowed once in 2005 and 2006 and had not been burned by the time of sampling.

The study fields, Harmison, Orbweaver, and Production, were in annual crop production the year before planting and were treated with herbicide (glyphosate and 2,4-D) prior to planting. The fields differ in soil type (Nestrud and Woster 1979) and topography. Production is relatively flat and consists of Aquertic Argiudolls formed in loess. Orbweaver is also relatively flat and consists of Oxyaquic Argiudolls formed in loess. Finally, plots at Harmison are divided into two sections and situated on south and north facing slopes on Mollic Hapludalfs formed in glacial till. For more sampling details and a complete species list see Chapter 3 (Yurkonis et al. In press-a)

Data collection

A 1 m² sample quadrat was established in a random location to the north of the central marker in each plot. All species were recorded and species relative abundance measured through point intercept sampling with 40 pins dropped uniformly across the quadrat. A small value (0.5 touch) was added for each species that was present but was not touched by a pin when calculating relative abundance and diversity measures. Relative abundance was calculated by dividing the total touches for species i in a quadrat by the total touches in the quadrat. These data were used to calculate richness (R) and evenness ($[1/D]/R$) of sown species, where $D = \sum p_i^2$ and p_i = relative abundance of species i . Invader relative abundance was calculated by dividing the total touches for non-sown exotic and native species by the total touches in the quadrat. Exotic and non-sown species were combined because all likely established from the local species pool post-seeding.

To quantify plant arrangement we mapped the positions of each species throughout each quadrat by dividing quadrats into 64– 12.5 x 12.5 cm cells and recording the identity of the species occurring within each cell. This cell size falls within the range of typical plant densities in a remnant tallgrass prairie (Losure et al. 2007) and was generally an appropriate scale for capturing ramets of a single species in each cell. In cases where ramets of multiple species were rooted in the same cell we recorded the identity of each species. From these data we generated a fine-scale map (resolution = 12.5 x 12.5 cm) of the locations of each species throughout the quadrat and determined how many separate patches were occupied by each species with the program QRULE (Gardner 1999, Gardner and Urban 2007). A patch was defined as a group of adjoining map cells occupied by the same species, where adjoining cells could be directly adjacent to or on the diagonal from one another (Turner et al. 2001).

Two metrics describing plant arrangement were computed based on these patches for each species in each quadrat. We described the mean area occupied by ramets of each species with the mean area-weighted patch size ($\sum S_{ik}^2 / \sum S_{ik}$) metric, where S_{ik} is the size (m^2) of the k th patch of species i . Computing mean patch size in this way reduces the effects of small patch sizes on the overall mean (Turner et al. 2001). The second metric was patch mean-squared radius (hereafter dispersion) which is a measure of within patch dispersion in meters where larger mean-squared radius values indicate that a larger area is needed to encompass the patch than one with smaller values (Gardner 1999).

After computing these metrics at the species level, we found the mean for both metrics across all species in a quadrat and used these values in the final analyses. Thus the mean patch size for the quadrat describes the average size of a patch of conspecific ramets of any species in a quadrat. A higher mean patch size indicates that any given group of conspecific ramets occupied a larger continuous portion of the ground surface than in a quadrat with a lower value. The quadrat-scale patch dispersion metric describes the spatial extent of any given patch in a quadrat, where higher values indicate that conspecific ramets in a patch are spread over a greater area (but may not necessarily occupy more ground surface) than in quadrats with smaller values.

Data analysis

Multivariate ANOVA was used to test for differences among fields and for the effect of seeding method on community structure and invader abundance. For these and subsequent analyses mean patch area-weighted size, mean patch dispersion, and species richness were natural log transformed and invader abundance arcsin squareroot transformed to improve normality. Pearson correlation was used to assess the bivariate relationships among the

transformed community structure metrics and invader abundance values. A principle components analysis (PCA) based on the correlation matrix was used to show the relationships among the community structure metrics for each field. Two plots were excluded in the Orbweaver analyses because no species from the seed mix were present in the quadrats. Assumptions of linearity among the variables (McCune and Grace 2002) were met for the Orbweaver and Production fields but not the Harmison field. In the Harmison field there was a significant non-linear (2nd order) relationship between species richness and size and invader abundance and area weighted patch size. To meet the assumptions of linearity we restricted all of the Harmison analyses to plots with area-weighted mean patch sizes of less than 0.09 m² (n = 20). All analyses were conducted in SAS (version 9.1, SAS Institute).

We used multi-group path analysis in Amos 5.0 (Arbuckle 2003) to confirm (Grace 2006) our theoretical model (Figure 4.1) of the relationships among species richness, evenness, plant arrangement, and invader relative abundance. We included a covariance term in the structural equation model to account for the potential negative correlation (Wilsey *et al.* 2005) between species richness and evenness. Arrangement was modeled as a linear function of richness and evenness and invader abundance was modeled as a linear function of richness, evenness, and arrangement in a saturated model (Grace 2006). Area weighted patch size was used as the sole arrangement metric because patch size was highly correlated with dispersion. With such an analysis we are unable to separate cause versus effect and restrict our analysis to explaining the associations among species richness, evenness, arrangement, and invader abundance at a single point in time. The assumptions of linearity, normal residuals, multivariate normality, and convergence were met for all three fields. Our analysis

used *t*-tests to determine if unstandardized paths coefficients (based on maximum likelihood estimation of the model parameters and their standard errors) were significantly different from zero. We also tested if unstandardized direct, indirect, and total effects were significantly different from zero using Monte Carlo simulation (based on 1,000 bootstrap samples) to estimate the standard errors and confidence intervals for each effect. A mutligroup analysis allowed us to test for pairwise and overall differences in path coefficients among fields by constraining path coefficients to be equivalent. Pairwise comparisons with a *t*-value greater than 1.96 were interpreted as significantly ($p < 0.05$) different from zero. Standardized path coefficients, which indicate how many standard deviations a response variable is expected to change given a unit change in an explanatory variable (Grace 2006, Van Riper and Larson 2009), from the unconstrained model for each field are presented.

Results

After three growing seasons, plots in the three fields differed in quadrat-scale evenness, plant arrangement, and invader abundance (Table 4.1, 4.2). Conspecific ramets were arranged into smaller patches and sown species evenness was greater in Harmison and Orbweaver than in

Table 4.1 Untransformed mean (± 1 SD) diversity, plant arrangement, and invader relative abundance within each field at NSNWR.

Metric	Harmison (n = 20)	Orbweaver (n = 22)	Production (n = 24)
Patch size (m ²)	0.04 \pm 0.02	0.05 \pm 0.02	0.20 \pm 0.05
Patch dispersion (m)	0.15 \pm 0.01	0.16 \pm 0.02	0.21 \pm 0.03
Richness	6.85 \pm 3.03	5.68 \pm 1.84	5.83 \pm 1.52
Evenness	0.47 \pm 0.21	0.40 \pm 0.11	0.29 \pm 0.09
Invader abundance	0.37 \pm 0.32	0.20 \pm 0.17	0.08 \pm 0.09

Table 4.2 F-values from a MANOVA assessing effects of field identity and planting type on community structure metrics and invader abundance at NSNWR.

Metric	Field (F)	Planting type (P)	F x P
Patch size	144.78***	0.04	0.12
Patch dispersion	55.57***	0.49	0.08
Richness	0.56	3.02 [‡]	0.08
Evenness	8.45***	0.05	0.14
Invader abundance	11.02***	0.00	0.42
df	2,60	1,60	2,60
Pillai's Trace	18.37***	2.42*	0.53
df	10,114	5,56	10,114

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; [‡] $P < 0.10$

Production quadrats (Table 4.1, 4.2). Within these fields *Elymus canadensis* and *Andropogon gerardii* (Big bluestem) were the most abundant, planted species comprising, on average, 34% (Harmison) to 84% (Production) of the point intercept touches in a quadrat. *Setaria viridis* (Green bristlegrass) and *Taraxacum officinale* (Common dandelion) were the most common exotic invaders alongside the native *Conyza canadensis* (Canadian horseweed). Our scale for sampling arrangement was appropriate for capturing patches of conspecific ramets through the quadrat. The average number of sown species recorded per cell in Orbweaver was 1.13 ± 0.47 , Harmison 0.66 ± 0.77 , Production 1.22 ± 0.50 . Drill seeded quadrats (6.63 ± 0.37) contained more sown species than broadcast seeded quadrats (5.58 ± 0.38) and, as a result, there was an overall effect of planting type (Table 4.1). However, mean patch size and dispersion were similar between drill and broadcast seeded plots, suggesting that planting method did not affect the ways species generally established in space (but see Yurkonis et al. In press-a). As a result, planting type was not taken into account in the subsequent analyses.

Bivariate correlations among species richness, evenness, plant arrangement metrics, and invader abundance were mixed in significance among fields (Table 4.3). The arrangement metrics, patch size and dispersion, were consistently positively correlated and this was the only significant correlation in the Orbweaver quadrats. In the remaining fields species richness and evenness were negatively correlated as predicted. In the Production quadrats, patch size was negatively correlated with richness and, contrary to predictions, positively correlated with evenness. These relationships were reversed in the Harmison quadrats where patch size was positively correlated with richness and negatively correlated with evenness. Finally, Harmison was the only field where community structure metrics were correlated with invader abundance.

Table 4.3 Pearson correlation coefficients (r) among sown species richness, evenness, plant arrangement metrics, and invader abundance in each field at NSNWR.

Field	Dispersion	Richness	Evenness	Invasion
<i>Harmison</i> ($n = 20$)				
Patch Size	0.89***	0.76***	-0.71***	-0.80***
Dispersion		0.60**	-0.53*	-0.71***
Richness			-0.67**	-0.90***
Evenness				0.55*
<i>Orbweaver</i> ($n = 22$)				
Patch Size	0.91***	-0.41 [‡]	-0.39 [‡]	-0.31
Dispersion		-0.37 [‡]	-0.35 [‡]	-0.13
Richness			-0.13	-0.28
Evenness				0.30
<i>Production</i> ($n = 24$)				
Patch Size	0.91***	-0.83***	0.53**	-0.02
Dispersion		-0.75	0.66***	-0.03
Richness			-0.64**	-0.22
Evenness				0.34

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; [‡] $P < 0.10$

The degree to which plant arrangement metrics were dependent on species richness and evenness varied among fields (Figure 4.2). For the Orbweaver field quadrats, the PCA of sown species richness, evenness, and arrangement metrics had two eigenvectors > 1 which explained 58% and 28% of the variation among quadrats respectively (Figure 4.2). Here, all three metrics were roughly orthogonal (90° angles between any two metrics) to one another

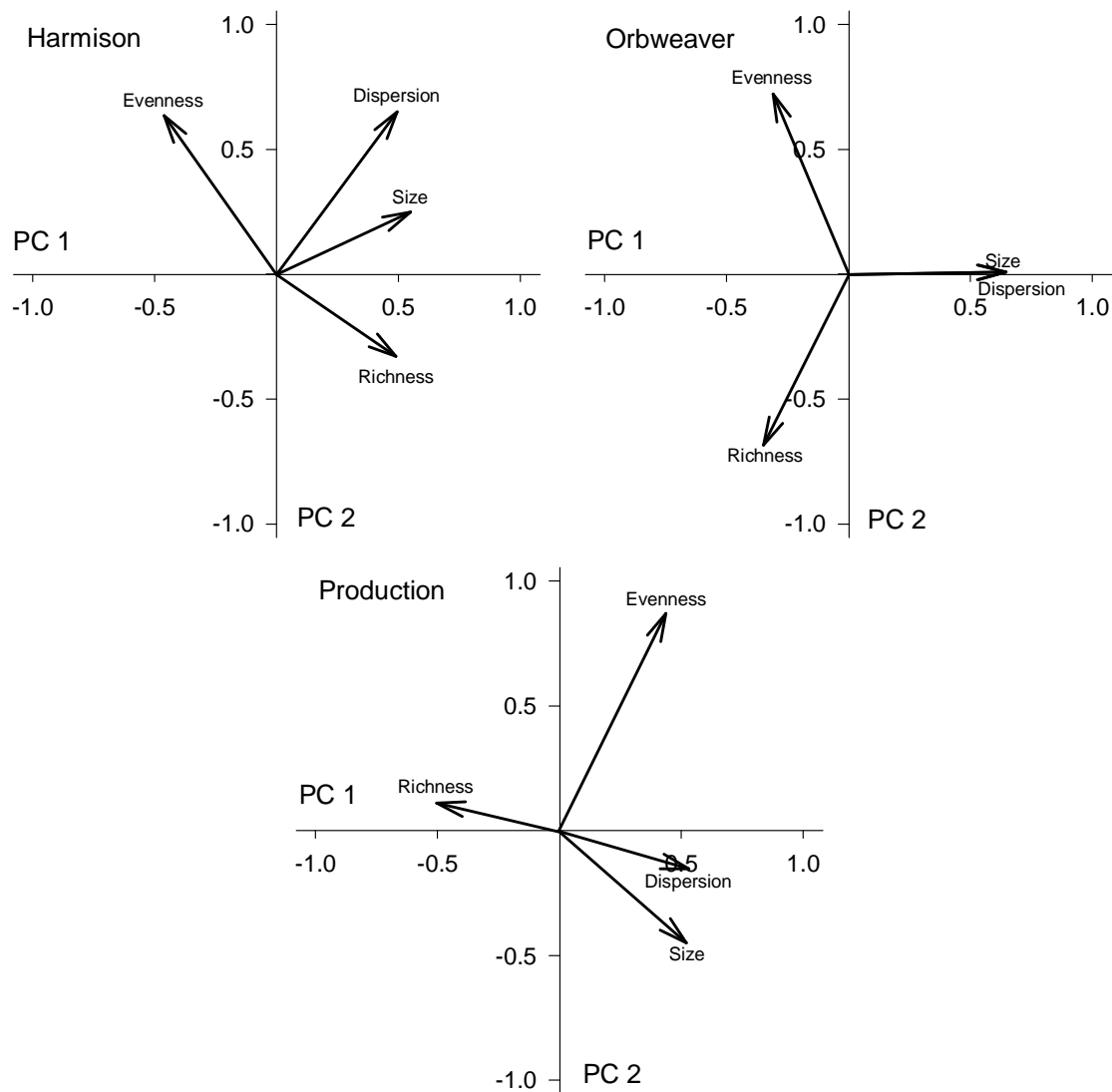


Figure 4.2 Principle components analysis of sown species richness, evenness, and arrangement metrics in each field at NSNWR.

along the first two eigenvectors. In the Harmison and Production fields the arrangement metrics were dependent on richness and evenness. In the Harmison field, where there was one eigenvector greater than one, explaining 77% of the variation among quadrats (the second is shown for reference), arrangement variables were positively related to richness and negatively related to evenness. In the Production field, where there was also one eigenvector greater than one, which explained 80% of the variation among quadrats, arrangement variables were positively related to evenness and negatively related to richness.

Path analysis

The magnitudes of the unstandardized path coefficients were significantly different among fields for three of the five paths in our model and, thus, the models were not similar across fields ($X^2 = 51.1$, $df = 10$, $p < 0.001$, Figure 4.3). The magnitudes of the evenness path coefficients were most variable among the fields. The path coefficients between evenness and invader abundance differed between Harmison and Production ($t = -2.132$) and the path coefficients between evenness and patch size differed between Production and Orbweaver ($t = -2.223$). The path coefficient between species richness and patch size was also significantly greater in Harmison than in the remaining fields (Orbweaver: $t = 3.849$, Production: $t = 5.922$). Interestingly, the magnitudes of the path coefficients between arrangement and invader abundance and richness and invader abundance were consistent among fields ($t < |1.96|$).

Despite differences in the magnitude of the path coefficients, there were some consistent trends in the significance of the direct effects among fields (Table 4.4, Figure 4.3). First, evenness did not have a direct effect on invader abundance in any field, despite considerable variability in evenness among quadrats within each field (Table 4.2). Secondly,

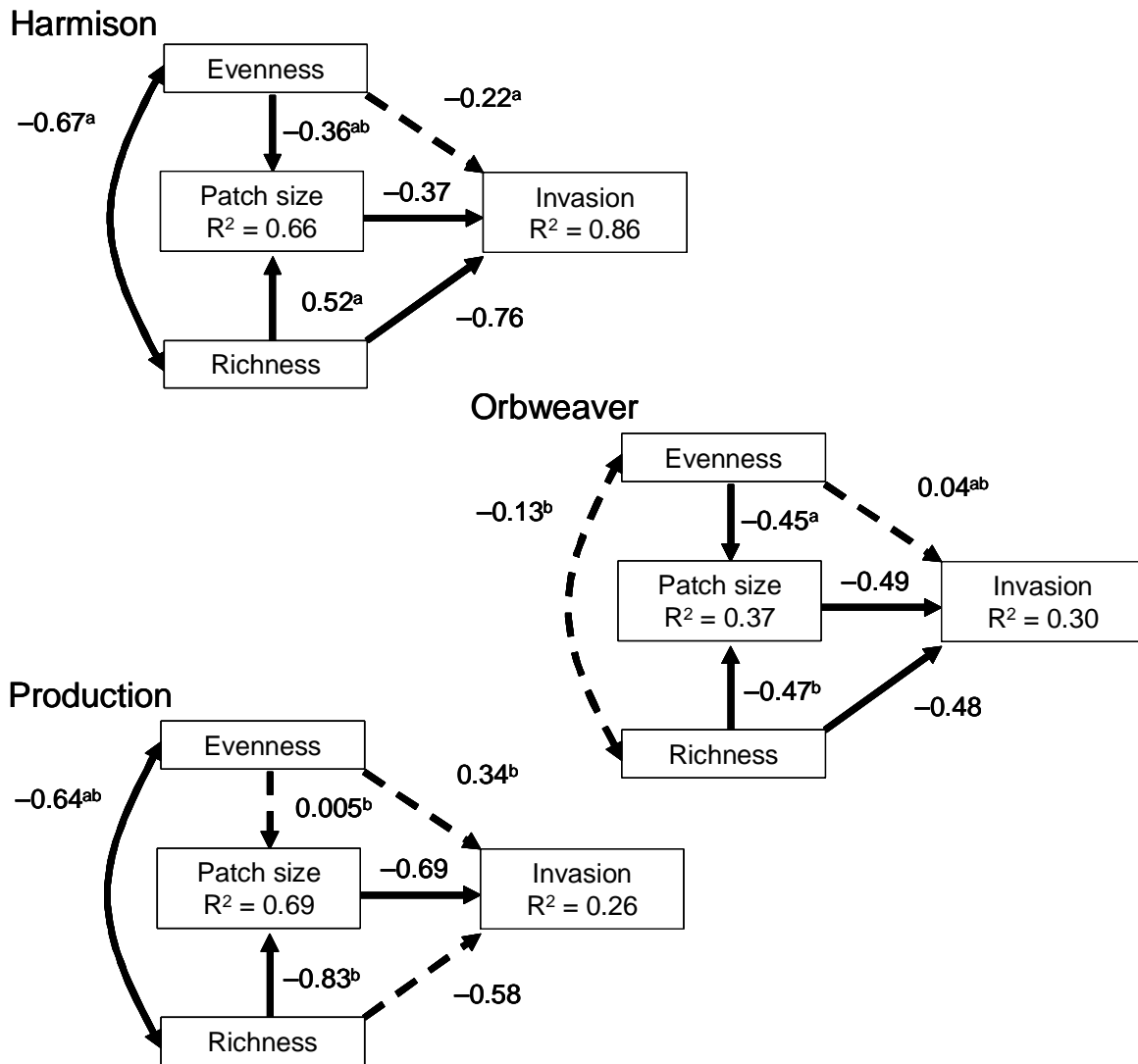


Figure 4.3 Path analyses of the relationships among plant arrangement metrics, species richness, evenness, and invader abundance with standardized coefficients. Paths with unstandardized coefficients significantly different from zero are indicated with solid lines and non-significant with dashed lines. Paths that are significantly different among fields in pairwise comparisons are indicated with different letters.

Table 4.4 Summary of standardized direct, indirect, and total effects of species richness, evenness, and patch size on invader abundance from the path analyses. Significance is based on Monte Carlo bootstrapping of unstandardized effects.

Predictor	Direct	Indirect	Total Effect
<i>Harmison (n = 20)</i>			
Evenness	-0.22	0.13*	-0.089
Species richness	-0.76**	-0.19*	-0.96**
Patch size	-0.37*		
<i>Orbweaver (n = 22)</i>			
Evenness	0.04	0.22*	0.26
Species richness	-0.48*	0.23*	-0.25
Patch size	-0.49*		
<i>Production (n = 24)</i>			
Evenness	0.34	-0.0033	0.33
Species richness	-0.58	0.57*	-0.011
Patch size	-0.69 [‡]		

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; [‡] $P < 0.10$

richness was consistently related to patch size, although the direction of this relationship changed among fields. In Harmison, richness was positively related to patch size, while in Orbweaver and Production richness was negatively related to patch size. Finally, in contrast to our predictions, patch size was negatively related to invader abundance when controlling for the common effects of species richness and evenness in each field. Quadrats with large conspecific patches were less invaded than quadrats with small conspecific patches. With one exception, significance of direct effects from Monte Carlo bootstrapping (Table 4.4) was consistent with the maximum likelihood based significance tests (Figure 4.3). The effect of patch size on invader abundance was marginally significant ($p = 0.054$) in the bootstrapping analysis and significant ($p = 0.034$) in the maximum likelihood analysis, which reflects an 8% increase in the standard error estimate (average across all direct effects = 10%) in the bootstrap analysis.

Effects of richness and evenness on patch size translated into interesting indirect effects that were masked in the bivariate correlation and PCA analyses (Table 4.4). In Harmison and Orbweaver, the fields with smaller patch sizes (Table 4.2), there was a significant negative effect of evenness on patch size which resulted in a significant indirect effect of evenness on invader abundance. As evenness increased invader abundance also increased, but this effect was only apparent when taking into account the fact that as evenness increases patch size decreases in these fields.

There were also significant indirect effects of richness on invasion via patch size in all three fields, although the direction of the indirect effect was variable. In Harmison, a negative direct effect of richness on invader abundance was magnified by an indirect effect via patch size. This resulted in a significant total effect of richness on invader abundance which supports findings from the bivariate correlations. Here, richness was inversely related to invasion because invader abundance decreased with increasing richness and because high richness quadrats had larger patch sizes and thus lower invasion. For Orbweaver, a negative direct effect of richness on invader abundance was countered by a positive indirect effect of richness on invader abundance due to effects of patch size. As richness increased the proportion of invaders decreased. However, when the effects of richness on patch size are taken into account we found that as species richness increases the proportion of invaders increases. This results in a non-significant total effect of richness on invasion, again supporting the bivariate correlation. Finally, in Production the only effect of richness on invasion occurred when taking into account the relationship between richness and patch size. As richness increased, patch size decreased and thus invasion increased. In this field there was no relationship between richness and invasion and no total effect of richness on invasion.

Regardless of the direction of the indirect effects, it is clear that the effects of richness and evenness can be explained in part by the relationship between these metrics and patch size.

Discussion

The ways species occupy space in a study area is an additional and potentially important aspect of community structure which may affect communities independently of effects attributable to the number and relative abundances of resident species. Relationships among species richness, evenness, and plant arrangement metrics showed consistent trends across three fields of grassland plots. Richness was consistently related to mean patch size, a measure of plant arrangement, while evenness was related to patch size in two of the three study fields. Despite dependency on species richness and evenness, plant arrangement still had a direct (negative) effect on invasion when controlling for species richness and evenness that was similar in magnitude across all fields. Finally, richness and evenness had some effect on invader abundance due to their relationships with patch size in each field. Thus, arrangement of sown species was related to invader abundance in each field but this effect was not apparent when assessing the bivariate correlations. Our results suggest that metrics that assess plant pattern may more consistently predict invasion than species richness or evenness metrics, and partitioning the effects of community structure in this way would separate effects of variation in diversity versus plant pattern in diversity- invasion studies.

Relationships among metrics of community structure

Bivariate correlations among species richness, evenness, and patch size were mixed among fields. Species richness and evenness were independent to negatively correlated which supports additional studies that have found weak negative relationships at this scale in grasslands (Wilsey et al. 2005). When considered in the context of this relationship between

richness and evenness, species richness was always related to patch size while evenness was in two out of three cases. Mean patch size, whether of ramets from one or multiple conspecific individuals, was consistently correlated ($R^2 = 37\%$ to 69%) to one or both of the common diversity metrics.

The prediction that evenness would be negatively related to patch size was supported in two of the three fields. This suggests that evenness may, but does not necessarily, account for the ways plants occupy space within a study plot. There are two potential reasons for this outcome. First, the ways species occupy space may affect peak growing season evenness. We investigated these plots to determine if evenness can be used to explain the ways species occupy space. Similarly, the ways species occupy space may affect interactions among individuals and their relative abundances (Stoll and Prati 2001, Racz and Karsai 2006). However, results from an experimental study investigating this pathway in grassland plots suggest that plot-scale evenness is relatively insensitive to initial plant arrangement (Chapter 5). Alternatively, as individuals develop during the growing season from their rooted locations, their canopies begin to overlap (Spehn et al. 2000). By the peak of the growing season the space they fill aboveground may not be proportional to the rooted area occupied by any individual due to species differences in aboveground biomass allocation and architecture.

Unlike evenness, species richness was consistently related to mean patch size. However the direction of this relationship was variable. In two of the three fields, our prediction that species rich quadrats would contain species distributed into small patches was supported. Establishing seedlings may have been limited in space due to interactions with other species or due to potentially greater resource heterogeneity in species rich areas

(reviewed in Grace 1999, Lundholm and Larson 2003). In the third field, species rich plots contained species aggregated into large patches. This could result from interspersions among planted species at scales less than 12.5 x 12.5 cm in this field. However, this does not appear to be the case as this field had the lowest number of planted species recorded per map cell. Alternatively, sites conducive to establishment of the planted species in the Harmison field may also have been sites where planted species could spread more readily than sites that were not.

In general, our findings suggest that plant arrangement, as measured by mean patch size, may be explained by species richness and evenness. Assuming there is no direct effect of arrangement on invasion resistance and that indirect effects of richness through species arrangements are minimal, these findings suggest that one would only need assessments of species richness and evenness to assess effects of community structure on invader abundance in this study. However, additional findings suggest that this assumption may not always be met and plant arrangement contributes to explaining invader abundance.

Describing invader abundance

Our results support the general notion that species rich locations are less invaded (Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002), but did not support our hypotheses concerning the effects of evenness on invasion at this scale. In two fields, high species richness was associated with low invader abundance. However, this relationship was only apparent through the path analysis when we partitioned richness into effects attributable to the number of species present versus effects attributable to the ways they occupy space and allowing correlation between species richness and evenness. This finding of a direct negative effect of local richness on invasion is consistent with others that have considered the

relationship between species richness and invasion at this scale (Tilman 1997, Naeem et al. 2000). However, as with Kennedy et al. (2002), our results suggest that effects of richness on invasion due to the presence of multiple species may be confounded with effects of how species physically occupy space.

Contrary to predictions from other experimental and observational studies (Wilsey and Polley 2002, Smith et al. 2004, Tracy and Sanderson 2004, Losure et al. 2007), we did not find that evenness was directly related to invasion. Wilsey and Polley (2002) varied evenness while keeping richness constant in four species experimental communities and found that invasion decreased with increasing evenness early and late in the season. Smith et al. (2004) manipulated dominance of abundant species and species richness by removing rare species from remnant grassland plots and found that invasion was reduced when evenness was increased through biomass removal, but not when species richness was altered. Finally, in a wide survey of the effects of evenness on invasion in pastures, Tracy and Sanderson (2004) found that weed abundance was lower in more even communities. While we may find that changes in evenness affect invasion in experimental or well established communities, these metrics were not related under realistic conditions in the young reconstructed communities that we sampled. This may be because the relationship between evenness and invasion could be most pronounced transitioning from moderate to high evenness communities, which were not well represented in our study. We had a narrower range of evenness values (0.2 to 0.7 overall) than in the aforementioned studies (0.3 to 1.0), which included high evenness communities. Additionally, experimental studies have shown that the identity of the dominant species may also affect the nature of the evenness – invasibility relationship (Emery and Gross 2007, Mattingly et al. 2007). Restored tallgrass

prairies often have high species turnover among plots (Martin et al. 2005) and thus the dominant species in each plot may have differed. However, this was not likely the case in our study. The seed mix and resulting plantings were generally dominated by *Elymus canadensis*, which has previously been shown to reduce invasion with increasing abundance in similar communities (Emery and Gross 2007). Finally, the relationship between species relative abundances and invasion at peak biomass in this system may not be indicative of the effects of species relative abundances on the invasion process at other times of the season (Wilsey and Polley 2002, Losure et al. 2007).

Most interestingly, our results suggest that plant arrangement independently explains invasion when controlling for common influences of richness and evenness. This is likely because the net neighborhood effect (Naeem et al. 2000, Kennedy et al. 2002, Milbau et al. 2007) is more closely depicted with this measurement of community structure than with richness or evenness measures that focus on identity and variation among species in size but not their local effects on microsites. However, contrary to our predictions, larger patch quadrats were less invaded than smaller patch quadrats. A negative relationship between patch size and invasion may result from several factors. This could result from resident species overlapping more in large patch quadrats. However, because there was generally one species per cell, this was not likely. Alternatively, the direction of this relationship was determined by the identity of the dominant species, much like has been proposed for evenness effects (Emery and Gross 2007, Mattingly et al. 2007). The cool season grass *Elymus canadensis* was abundant through space and may have inhibited early and late season invasion due to development of a dense litter layer (Emery and Gross 2007) or due to shared phenology with invading cool season invader species (Fargione et al. 2003, Losure et al.

2007). Future studies need to determine if relationships between arrangement and invasion vary across dominant species (e.g. Emery and Gross 2007).

The final step in examining the effect of plant arrangement on invader abundance is to consider the indirect effects of species richness and evenness that occur as a result of their relationships with plant arrangement (Table 4.4). In two fields, evenness was positively associated with invasion due to indirect effects of patch size. In all three fields, species richness was associated (positively in two and negatively the third field) with invasion due to indirect effects of patch size. While others have found positive effects of richness on invasion at larger scales (Levine and D'Antonio 1999, Stohlgren et al. 1999, Levine 2000), this is the first study to find both positive and negative relationships between richness and invasion at the quadrat-scale. Generally, positive relationships are predicted between richness and invasion when assessing this relationship in heterogeneous locations, while a negative relationship is predicted when assessing the relationships at a finer scale in supposedly more homogeneous locations (Levine and D'Antonio 1999, Hooper et al. 2005). Our findings suggest that heterogeneity may affect invasion at all scales, either positively or negatively, and that the total effect of richness and evenness on invasion arises from effects of local heterogeneity and diversity on invasion. This suggests that in studies reporting relationships between species richness and invasion, species arrangement and true richness effects may be confounded in bivariate analyses, even in studies with initially randomly distributed individuals. Of course, the direction of this effect would likely depend on the identity of the dominant species and if species effects on establishment are more localized or diffuse.

Conclusions

Overall, we found that no one aspect of community structure explains invader abundance when assessed with bivariate correlation, but when collectively considered through the framework presented in Figure 4.1 both species richness and plant arrangement were related to invasion, whereas evenness was not. Although species richness correlates with local invasion, our findings suggest that the effects of species richness and evenness on invasion may be partitioned into direct effects and indirect effects arising through diversity effects on plant pattern. Our understanding of the effects of species richness and evenness on invasion may be accelerated by considering species arrangement in the framework presented here, both in management and when investigating diversity-invasion relationships.

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**CHAPTER 5. INITIAL PLANT ARRANGEMENT AFFECTS INVASION
RESISTANCE IN EXPERIMENTAL GRASSLAND PLOTS**

A paper to be submitted to *Ecology*

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Abstract

The ways plants are arranged with respect to one another may affect community dynamics in ways that are independent of effects attributable to species richness or abundances. To test if initial plant arrangement affects species composition and invasion in a perennial system, 24 – 4 m² plots were planted with transplants of four common grassland species in various arrangements while controlling for plot-scale species richness and abundances. Plots varied along a gradient of initial patch size, where conspecific individuals ranged from occurring in several small groups (patches) dispersed through the plot to occurring in fewer, larger groups. We tested the hypotheses that planted species evenness would be higher, the light environment would be more heterogeneous, and invader abundance would be highest in plots with initially larger conspecific patches. Evenness did not vary along the initial patch size gradient. Early in the second growing season mean light at the soil surface was greater and the light environment at the soil surface was more heterogeneous in plots with initially larger conspecific patches. Furthermore, invader abundance was consistently greater in plots with initially larger conspecific patches than those that were planted with smaller conspecific patches. However, invader abundance was not correlated with mean light at the soil surface or heterogeneity in the light at the soil surface, suggesting that effects of plant arrangement on invasion were not due to differences in the light environment established with increasing

patch size. Our findings support the hypothesis that invasion increases with increasing fine-scale heterogeneity, but, at this point, it is unclear through what mechanisms this occurred.

Introduction

Communities differ from one another in the number (species richness) and abundances (evenness) of constituent species and both of these attributes affect aspects of diversity maintenance and local invasion (reviewed by Hooper et al. 2005, Hillebrand et al. 2008). Communities may also differ in the ways conspecific and heterospecific individuals are arranged with respect to one another (e.g. Greig-Smith 1979, Glenn and Collins 1990, Thorhallsdottir 1990, Herben et al. 1993, Bartha et al. 1995, Purves and Law 2002, Overton and Levin 2003, Yurkonis et al. In press-b) and this plant arrangement may independently affect diversity maintenance and invasibility (Watt 1947, Tilman and Kareiva 1997, Murrell et al. 2001, De Boeck et al. 2006). Although empirical studies have shown that varying plant arrangement affects competitive interactions among neighboring individuals in annual systems (Norris et al. 2001a, Stoll and Prati 2001, Monzeglio and Stoll 2005) and coral assemblages (Idjadi and Karlson 2007, Hart and Marshall 2009), the coarser-scale effects of plant arrangement have not been empirically tested in species rich perennial grasslands where many studies of the controls over diversity maintenance and invasibility have occurred.

Varying fine-scale (within plot) plant arrangement while maintaining the same coarser-scale (plot) species richness and evenness may affect plot-scale dynamics via two pathways. First, varying initial plant arrangement may affect plot-scale species composition by altering interactions among and thus abundances of resident species. Effects of individual plants on others are often restricted to scales finer than typical plot-scales (Czaran and Bartha 1992, Casper et al. 2003, Murrell and Law 2003, Vogt et al. 2010). Thus, individuals most

likely interact with their immediate neighbors, but they may not interact with all of the individuals in a plot. It is also well established that plant performance is influenced by the density and identity of neighboring plants (Ross and Harper 1972, Mack and Harper 1977, Goldberg 1987). Plants surrounded by conspecific neighbors often produce less biomass than plants surrounded by heterospecific neighbors, either because competition is reduced or facilitation increased when individuals are surrounded by heterospecifics (Isbell et al. 2009). Increasing conspecific interactions by initially arranging conspecific individuals into fewer, larger patches as opposed to several, smaller patches may result in reduced abundance for some species. However, in cases where species strongly differ in their dispersal and competitive abilities, a weaker competitor may be more abundant when individuals are grouped into fewer, larger patches (Molofsky 1994, Bolker and Pacala 1997, Bolker and Pacala 1999, Law and Dieckmann 2000, Racz and Karsai 2006). In this case, altering arrangement may prevent, or at least delay, competitive exclusion of some species by either reducing negative heterospecific interactions for some species or by increasing negative conspecific interactions for others (Rees et al. 1996, Murrell et al. 2001, Stoll and Prati 2001, Idjadi and Karlson 2007, Hart and Marshall 2009). In either case, if such neighborhood interactions affect species performance, changing fine-scale plant arrangement (the number and size of groups of conspecific individuals) while maintaining initial plot-scale density and diversity (richness and evenness) should affect species composition and the evenness component of diversity.

The effects of plant arrangement on species coexistence have only been tested in a few cases. Stoll and Prati (2001) manipulated arrangements of annual species and found that arranging individuals into large conspecific patches facilitates persistence of weaker

competitors. These findings were further supported by studies of the effects of spatial arrangement in tomatoes and barnyard grass (Norris et al. 2001a) and most recently for corals (Idjadi and Karlson 2007, Hart and Marshall 2009). Hart and Marshall (2009) manipulated the arrangement of individuals of four coral species and found that some species occupied more area when conspecific individuals were grouped into four large patches than when they were randomly arranged. Over short time-scales, these experimental results generally support the hypothesis that when species differ in their relative tolerances of conspecific and heterospecific interactions, altering fine-scale arrangement while maintaining coarser-scale richness and evenness may affect diversity. Despite a long-standing interest in how pattern influences process in perennial systems (e.g. Watt 1947, Skellam 1952), this hypothesis has not been tested in species-rich perennial plant communities (Bolker and Pacala 1999, Bolker et al. 2003).

Varying fine-scale plant arrangement may also affect invasion at the plot-scale (Bergelson 1990, Olsen et al. 2005, De Boeck et al. 2006). Establishment in a site is generally determined by the density and identity of neighbors around the site (Fowler 1988, Bergelson et al. 1993, Herben et al. 2007, Milbau et al. 2007). Establishment is typically greater in sites surrounded by individuals of a few species than in sites surrounding by individuals of several different species because resources in these low-richness sites are not as completely consumed (Grubb 1977, Naeem et al. 2000, Loreau and Hector 2001, Kennedy et al. 2002). Altering plant arrangement within a plot would affect the availability of such low-richness sites for invasion. Plots with individuals arranged into large, single species patches contain more low richness sites and, thus, may be less resistant to invasion than a similar plot containing conspecific individuals arranged in several, smaller patches.

To determine if invaders are responding to such variation in the resource environment we can assess effects of plant arrangement on resource availability. In grasslands, light availability often affects invasion success, where establishment is more likely to be successful in locations where more light reaches the soil surface (Milbau et al. 2005, Losure et al. 2007). Thus, light availability at the soil surface may be used as a proxy for understanding potential establishment sites for invaders. Because light use should be lower in low-richness than high-richness sites (Spehn et al. 2000, De Boeck et al. 2006), mean light use at the plot-scale should be lower in plots with fewer, larger patches than in plots with more, smaller patches. If invaders are responding to the light environment, lower mean light use should be correlated with higher subsequent invader abundance. Because species often differ in the ways they use light, arranging individuals into large, single-species patches may also result in greater heterogeneity in the light environment within a plot. Greater heterogeneity in the light environment may also result in greater invasion, as conditions may be appropriate for establishment at more locations than in plots with a more homogeneous light environment (Derner and Wu 2004).

In addition to affecting the resource environment for invasion, plant arrangement may also affect how an invader spreads through an area once established (Bergelson et al. 1993, With 2002, 2004). If similar unoccupied sites are located near the establishment site, as would occur when individuals are arranged in large conspecific patches, an invader may more quickly colonize those sites than if similar unoccupied sites were further away, as would occur when individuals are arranged in small conspecific patches. Thus, invaders may be more abundant when conspecific individuals are arranged into fewer large patches than if

the resident plants were arranged in more small patches because plant arrangement facilitates dispersal of established invaders.

Although fine-scale plant arrangement may affect invasion in perennial systems, only a few studies have considered effects of resident plant arrangement on invasion. Bergelson (1990) manipulated arrangements of *Poa annua* and found invasion by two annual weeds was higher when individuals were planted in large conspecific patches than when individuals were randomly arranged due to inhibition of invader establishment by litter. Olsen et al. (2005) found that crop planting pattern affected weed recruitment, where weeds were less abundant when wheat was planted in a uniform pattern over rows. However, we are not aware of any studies that have manipulated arrangement among multiple species to test this effect on coarser-scale invasion.

Within this study we manipulated fine-scale plant arrangement while maintaining plot-scale species richness and evenness to test the effects of altering initial arrangement on evenness and invasion. We test the hypotheses that (1) evenness will be higher, (2) the light environment will be more heterogeneous, and (3) invader abundance will be greater in plots where conspecific individuals occur in fewer, larger patches than in plots with more, smaller patches. Our findings contribute to our understanding of how fine-scale plant arrangement may affect subsequent community dynamics and have implications for how to manage plant communities.

Methods

In May 2006, we planted 24 plots (2 x 2 m with 2 m inter-plot spacing) with seedlings of four native species planted along a gradient of increasing initial patch size. Diversity was kept constant at the plot-scale by maintaining the same levels of richness and evenness. Plots

were planted at the Iowa State University Horticulture Research Station (Ames, IA) on glacial till derived Clarion fine loam soils. Mean annual temperature is 8.8°C and mean annual precipitation is 837 mm for the area. The site was originally dominated by *Bromus inermis* and was treated with glyphosate herbicide and disked prior to planting. Seedlings of two C₄ bunch grasses (*Andropogon gerardii* Vitman and *Schizachyrium scoparium* (Michx.) Nash) and two forbs (*Ratibida pinnata* (Vent.) Barnh. and *Monarda fistulosa* L.) that are common in local remnant grasslands (Martin et al. 2005) were grown in the greenhouse to approximately equal biomass in a 3:1 sterilized soil:sand mix. *A. gerardii* did not grow as well as the other species in the greenhouse and, as a result, seedling biomass differed among species at planting ($F_{3,20} = 4.72$, $P = 0.0119$). *A. gerardii* was smaller than *M. fistulosa* ($0.038 \pm 0.0007\text{g}$ vs. $0.117 \pm 0.029\text{g}$, $F_{1,20} = 6.49$, $P = 0.0192$) and *S. scoparium* ($0.151 \pm 0.030\text{g}$, $F_{1,20} = 13.09$, $P = 0.0017$). Seedlings were planted into bare soil in a grid (64 plants m^{-2}) with equal spacing among seedlings. The planting density mimicked typical plant densities in local remnant prairies (Losure et al. 2007). Seedlings were watered upon planting and individuals that died were replanted in early June 2006. During the first growing season, plots were weeded to ensure seedling establishment. In subsequent years, all volunteers were allowed to persist to test hypotheses about invasion resistance.

A unique planting map was generated for each plot with the program QRULE (Gardner 1999, Gardner and Urban 2007). QRULE uses the mid-point displacement algorithm (Saupe 1988) to generate maps based on the desired size of the output map, the proportion of each habitat class (species), and H, a correlation parameter, which varies from 0 to 1 (Gardner 1999). To make a map, QRULE essentially generates a 3-dimensional surface with a few, large plateaus or several, small peaks, depending on the H-value. A map

generated by setting the H-value to 1.0 typically contains fewer, larger plateaus than a similar map generated by setting the H-value to 0.0. To create a 2-dimensional map from this surface, cells at successive elevation intervals are assigned to a habitat class, depending on the number and proportion of the desired habitat classes (With and King 2004). For the purposes of this experiment, planting maps were generated by setting the H value to either 0.0 ($n = 8$), 0.5 ($n = 8$), or 1.0 ($n = 8$) with four habitat classes (species) in equal proportions. This approach generated a series of maps that ranged from having cells of the same identity arranged in several smaller groups (patches) to having fewer, larger groups (patches) (Figure 5.1).

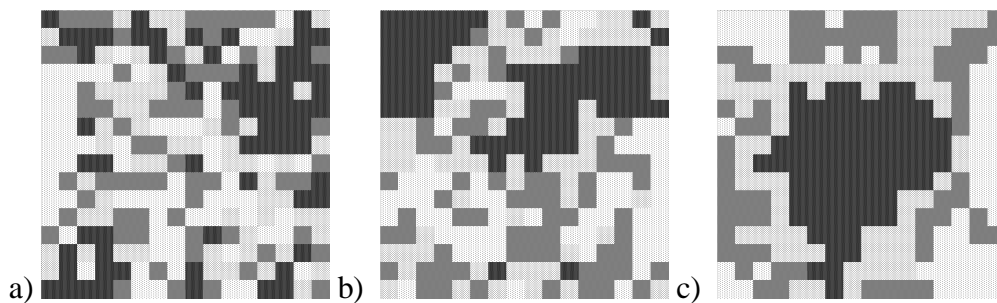


Figure 5.1 Representative planting diagrams for plots planted along a gradient of initial patch sizes. Each pixel represents one individual (256 plot^{-1}) of one of four common grassland species. A patch consists of a group of similarly colored adjoining cells. a) $H = 0.0$; mean area weighted patch size = 0.16 m^2 , b) $H = 0.50$; mean area weighted patch size = 0.40 m^2 , and c) $H = 1.00$; mean area weighted patch size = 0.68 m^2 .

We used the map analysis features in QRULE (Gardner and Urban 2007) to quantify initial plant arrangement within each planting map. The map analysis features were used to obtain the number of patches and the size of each patch of adjoining cells with the same identity within each map. A patch was defined as a group of adjoining map cells occupied by the same species, where adjoining cells could be directly adjacent to or on the diagonal from

one another (Turner et al. 2001) (Figure 5.1). Initial plant arrangement was quantified by calculating the area-weighted mean patch size ($\sum S_k^2 / \sum S_k$) across all of the patches in a plot, where S_k is the size of the k th patch in m^2 . This metric describes the mean area occupied by a group of individuals of the same identity when plots were planted. Large values indicate that conspecific individuals were arranged in fewer groups covering a larger area at planting than in plots with small values. Computing mean patch size in this way reduces the effects of small patch sizes (e.g. containing one or two individuals) on the overall mean (Turner et al. 2001). Figure 5.2 shows the distribution of the area weighted mean patch size variable for each input class and across all classes before and after natural log transformation to improve normality. Note that the transformed area weighted mean patch size variable differed among the map input classes ($F_{2,21} = 22.8$, $p < 0.001$), and that there was some overlap in the patch size distributions among classes. There are many ways to quantify spatial pattern in maps such as these (Riitters et al. 1995). We focus on this area-based metric in order to understand the consequences that arranging plants into large, conspecific patches, as often occurs in grassland restorations (Yurkonis et al. In press-a), has on community dynamics.

When planting, we consistently assigned species to each habitat class as generated in the QRULE output maps (each shade in Figure 5.1). Habitat classes one, two, three, and four were assigned to *A. gerardii*, *M. fistulosa*, *R. pinnata*, and *S. scoparium*, respectively. Thus an *A. gerardii* individual was more likely to be surrounded by *M. fistulosa* individuals than *S. scoparium* individuals (Type of neighbor, $F_{2,63} = 800.46$, $p < 0.01$). This difference was more pronounced in $H = 0.00$ versus $H = 1.00$ plots (Type of neighbor x H-value, $F_{6,63} =$

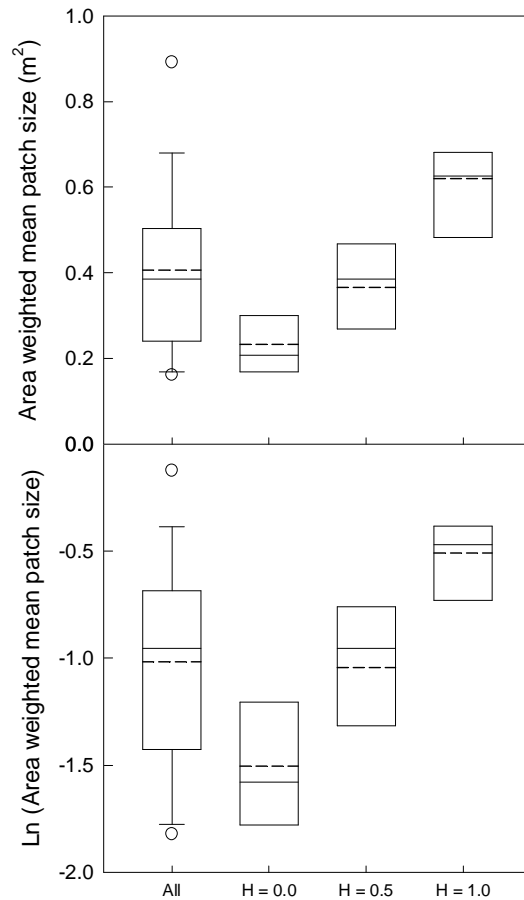


Figure 5.2 Box and whisker plots of the initial area-weighted mean patch size variable used as a measure of initial plant arrangement. Means are indicated by a dashed line. Separate plots are given for each map input class, 5th and 95th percentiles could not be calculated for these because of the sample size ($n = 8$). Distributions of the transformed variables are not significantly different from normal.

81.72, $p < 0.01$) as individuals in $H = 0$ plots were most likely to be surrounded by conspecific neighbors.

In late summer 2007, 2008, and 2009, species abundances were quantified with point-intercept sampling (Jonasson 1988) over the entire plot. In 2007 and 2008, a $1.5 \text{ m} \times 1 \text{ m}^2$ sampler was placed over each quadrant of the plot and a metal pin was dropped vertically through the vegetation at 10 cm intervals (40 pins per m^2). The number of times each species

i was touched by a pin was recorded. Species relative abundance was calculated by dividing the total touches for species i in a quadrat by the total touches in the quadrat for each sample year. These data were used to calculate evenness ($[1/D]/S$) of the planted species at the plot-scale, where $D = \sum p_i^2$, p_i = relative abundance of species i , and S = species richness (Smith and Wilson 1996, Wilsey et al. 2005). At the end of the 2008 growing season, aboveground biomass and litter were removed from each plot in a separate study to assess the utility of using point-intercept sampling to measure biomass-based diversity in these plots. In 2009, the same sampling method was used, but the number of sample points was reduced to 20 random locations in each quadrant to accelerate sampling. An analysis of the 2008 data indicated that reducing the number of sample points would not affect estimates of plot-scale diversity and invasion. The difference between evenness and invader abundance calculated from a sub-sample of the points in 2008 (20 randomly selected from each quadrant) and the full sample sampling effort was not significantly different from zero (Evenness: $t = 0.4045$, $p > 0.05$; Invader abundance: $t = 0.2341$, $p > 0.05$).

To test for effects of initial plant arrangement on the light environment we measured available photosynthetically active radiation (PAR) at the soil surface within each plot. In 2007 and 2008, above and below canopy PAR was measured monthly (May to August) at midday (10–2 CST) within each quadrant of a plot. A Decagon AccuPAR LP-80 Ceptometer (Pullman, Washington, U.S.A.) was used for the below canopy measurement and a Li-Cor external point sensor (Lincoln, Nebraska, U.S.A) for the above canopy measurement. The ceptometer was set to record the light reading at each of the 80 sensors arranged on the 90 cm probe inserted into the plot along the soil surface. Thus, plot soil surface PAR was measured at 320 points (4 x 80 sensors) at each sampling. The proportion

of available light that reached the ground surface was calculated by averaging the proportion of available light that reached the ground surface for each series of 80 measurements and averaging these values across the plot. Heterogeneity in the light environment was quantified by calculating the variance to mean ratio for each series of 80 measurements and averaging these values across the plot. Plots with lower variance to mean ratios have a more homogeneous light environment than those with higher variance to mean ratios.

Data analysis

To test for effects of initial plant arrangement on evenness and invader abundance in 2007, 2008, and 2009, we used a repeated measures ANOVA with area weighted mean squared patch size (hereafter mean patch size) at planting as a continuous effect (proc glm, SAS 9.2, SAS Institute). For these and subsequent analyses, mean patch size was natural log transformed and abundances arcsine squareroot transformed to improve normality. The plot with the largest initial patch size was excluded as an outlier (Figure 5.2) in the analyses presented here. Separate repeated measures ANOVA analyses were performed to test for differences in the response variables among the H input classes used to generate the planting maps. In these analyses (with the full data set), evenness and invader abundance were similar among the H input classes (results not shown), indicating that the conditions for generating the maps (setting the H-value to 0, 0.5, or 1.0) did not affect these responses *per se*.

To test for effects of plant arrangement on species composition, non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis distance matrix (Vegan package in R; Oksanen et al. 2007) was used to condense planted species abundances into axes describing the variation in plot-scale species composition in each year. Pearson

correlation (SAS 9.2) was used to test for correlation among mean patch size and plot scores on the first and second NMDS axes. Finally, mean (log transformed) and variance to mean ratio in the soil surface PAR were analyzed in separate repeated measures ANOVA (SAS 9.2) for 2007 and 2008 with mean patch size as a continuous effect. Correlation between the light environment and subsequent invader abundance was tested with Pearson correlation.

Results

Plot-scale evenness at planting was similar among the input classes ($F_{2,21} = 0.25$, $p > 0.05$; mean = 0.995 ± 0.0009) and did not vary with initial patch size ($F_{1,21} = 2.19$, $p > 0.05$). At the neighborhood-scale (based on the 8 neighbors surrounding 10 randomly sampled individuals from each plot), evenness was not correlated with initial patch size ($r = 0.15$, $p > 0.05$), but species richness was negatively correlated ($r = -0.83$, $p < 0.001$) and the probability of having conspecific neighbors was positively correlated ($r = 0.80$, $p < 0.001$).

Although plot-scale evenness at planting was not maintained after initial planting (Table 5.1), plot-scale evenness was similar among subsequent sample years ($F_{2,42} = 1.39$, $p > 0.05$) and did not vary along the patch size gradient ($F_{1,21} = 0.10$, $p > 0.05$, Year x Size: $F_{2,42} = 1.39$, $p > 0.05$, Table 5.1). As with evenness, initial patch size was not related to species composition. In each sample year, initial patch size was not correlated with the plot scores on an NMDS ordination of the planted species abundances (Table 5.2).

Invader abundance differed among years ($F_{2,42} = 51.28$, $p < 0.001$), increasing over time (Table 5.1). Although initial patch size had an overall effect on invasion ($F_{1,21} = 5.72$, $p < 0.05$), the nature of the relationship between patch size and invasion differed among years ($F_{2,42} = 3.65$, $p < 0.05$). Invader abundance was marginally related to patch size in 2007 ($F_{1,21} = 4.11$, $p = 0.06$) and positively related to initial patch size in 2008 ($F_{1,21} = 5.14$, $p <$

Table 5.1 Untransformed mean ± 1 SE plot-scale responses across all plots in an experiment assessing effects of altering fine-scale plant arrangement on plot-scale dynamics.

Parameter	2007	2008	2009
Evenness	0.72 \pm 0.025	0.81 \pm 0.023	0.70 \pm 0.023
Invader abundance	0.02 \pm 0.004	0.21 \pm 0.030	0.55 \pm 0.053
Light – mean			
May	0.042 \pm 0.0082	0.178 \pm 0.0099	--
June	0.034 \pm 0.0041	0.021 \pm 0.0028	--
July	0.081 \pm 0.0037	0.038 \pm 0.0029	--
August	0.075 \pm 0.0030	0.044 \pm 0.0031	--
Light – var/mean			
May	0.12 \pm 0.016	0.19 \pm 0.008	--
June	0.13 \pm 0.015	0.13 \pm 0.015	--
July	0.11 \pm 0.007	0.11 \pm 0.008	--
August	0.14 \pm 0.007	0.08 \pm 0.005	--

Table 5.2 Results from NMDS analyses of plot-scale planted species composition in 2007, 2008, and 2009. Pearson correlation was used to test for correlation between plot scores on each axis and initial patch size.

Year	# of runs	stress	Pearson correlation (<i>r</i>)	
			NMDS 1	NMDS 2
2007	10	12.48	-0.40 [‡]	-0.03
2008	11	14.47	0.33	0.43
2009	11	5.70	-0.10	0.23

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; [‡] $P < 0.10$

0.05) and 2009 ($F_{1,21} = 5.05$, $p < 0.05$; Figure 5.3) where plots with larger initial patch sizes had higher invader abundances than plots with initially smaller patches. The most abundant invaders included *Bromus inermis*, *Coronilla varia*, and *Conyza canadensis*, all of which were all present at the site prior to this study.

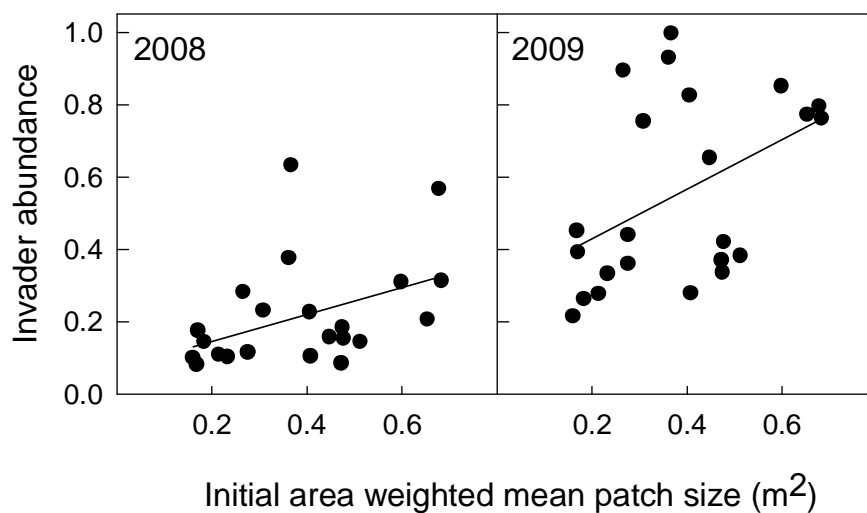


Figure 5.3 Effect of initial plant arrangement on invader relative abundance.

Light environment

Mean light at the soil surface was similar among months in 2007 ($F_{3,63} = 0.42$, $p > 0.05$), ranging from 3% to 8% of PAR in 2007 (Table 5.1). Mean light was related to initial patch size in 2007 ($F_{1,21} = 4.98$, $p < 0.05$), but this relationship differed among months (month \times size: $F_{3,63} = 3.04$, $p < 0.05$). In June 2007, mean light was positively related to mean patch size, but not in the remaining months (Table 5.3, Figure 5.4). In 2007, heterogeneity in the light environment differed among months ($F_{3,63} = 3.15$, $p < 0.05$) and was marginally related to patch size ($F_{2,21} = 3.94$, $p = 0.06$). As with mean light, there was an interaction between month and initial patch size ($F_{3,63} = 3.27$, $p < 0.05$), where the light environment in June was more heterogeneous in plots with larger initial patch sizes, but not in the remaining months (Table 5.3, Figure 5.4). Although there was a relationship between light and patch size and invasion and patch size, subsequent invader abundance was not correlated with the mean light or heterogeneity in the light at the soil surface in June 2007 (Table 5.4).

Table 5.3 F-values from ANOVAs assessing the effects of patch size on soil surface PAR.

Month	df	2007		2008	
		Mean	Var/Mean	Mean	Var/Mean
May	1,21	2.28	1.94	0.72	2.35
June	1,21	6.90*	7.68*	3.45 [‡]	0.00
July	1,21	1.49	1.22	0.73	0.67
August	1,21	1.06	0.01	0.00	0.09

* P<0.05; ** P<0.01; *** P<0.001, [‡] P < 0.10

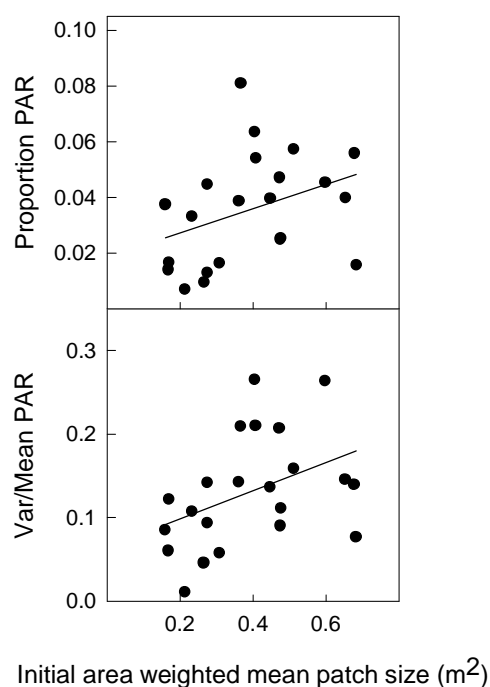


Figure 5.4 Relationship between initial patch size and the light environment in June 2007.

Table 5.4 Pearson correlation (r) between the soil surface light environment in June 2007 and subsequent invader abundance.

Light parameter	Invader abundance		
	2007	2008	2009
Mean PAR	0.32	0.32	0.28
Var/Mean PAR	0.12	0.27	0.36 [‡]

* P<0.05; ** P<0.01; *** P<0.001; [‡] P < 0.10

In 2008, mean light at the soil surface differed among months ($F_{3,63} = 10.07$, $p < 0.01$), ranging from 17% of PAR in May to 2% of PAR in June (Table 5.1), and was not related to initial patch size ($F_{1,21} = 1.46$, $p > 0.05$). As in 2007, there was an interaction between light and patch size ($F_{3,63} = 2.85$, $p < 0.05$), where light in June 2008 was marginally related to mean patch size, but not in the remaining months (Table 5.3). In 2008, heterogeneity in the light environment was similar among months ($F_{3,63} = 1.98$, $p > 0.05$) and not related to initial patch size ($F_{1,21} = 0.03$, $p > 0.05$; Month x Size $F_{3,63} = 0.68$, $p > 0.05$).

Discussion

We address the question does fine-scale plant arrangement affect species interactions and local invasion independently of plot-scale species richness and evenness? Invader abundance was higher in plots with initially larger conspecific patches and initial planting arrangement did not affect planted species evenness. Generally, initial heterogeneity in plant communities did not appear to affect resident species dynamics but may play a substantial role in regulating invasion. Thus, at least over the short term, plant arrangement appears to affect community stability not via effects on species coexistence, but by affecting invasion resistance.

We did not find evidence suggesting that fine-scale plant arrangement affects planted species coexistence at the plot-scale in this system. This result is somewhat consistent with a previous study by Lortie et al. (2005), which tested the effects of fine-scale plant pattern on plot-scale processes. Lortie et al. (2005) asked if finer-scale spatial pattern in plant density affects plot-scale characteristics and found that altering local density did not affect plot-scale mean plant size or survival in a desert annual system. In our study we manipulated arrangement of conspecific individuals while controlling density and found similar effects.

At least over a short time-scale, evenness did not appear to be affected by variation in initial plant arrangement.

Variation in initial plant arrangement may not have affected plot-scale evenness because individuals were not affected by the identity of their neighbors in this setting. When the transplants were planted, the extent of the influence of a single individual on others was likely limited to a scale much less than that of the plot. In a study assessing the scales of interaction among establishing calcareous grassland seedlings, individuals growing within 15 cm of one another affected the growth of one another (Vogt et al. 2010). If the scales of interaction were similar for the species in this study, the spacing used in this study (12.5 cm) likely resulted in some interaction among individuals at the time of planting and onward. Thus, at least initially, not all individuals were interacting with one another and their performance should have been affected by their neighbors. However, it is possible that effects of conspecifics and heterospecifics on focal plant performance were relatively equivalent for the species in this study (Goldberg and Barton 1992). If these effects were equivalent then altering arrangement would not affect species composition. Unfortunately, we do not have data concerning the relative tolerances of conspecific versus heterospecific interactions for these species, so it is unclear if this occurred.

Alternatively, the size of the neighbors may have had a greater effect than the identity of the neighbors on any given individual. Vogt et al. (2010) tested for differences between effects of conspecific and heterospecific neighbors on focal plant performance. They find that effects of conspecifics versus heterospecifics varies among species and suggest this interaction may be related to differences in size versus identity of the neighboring individuals (Vogt et al. 2010). In this case, performance in a neighborhood would be determined by

which individual was initially larger as opposed to the identity of the individuals present (Ross and Harper 1972). In our study, seedlings differed in initial size among species, so if initially smaller individuals were at a disadvantage then evenness should have declined, as occurred. However, evenness still should be related to initial arrangement as smaller individuals were more likely adjoining other small individuals and thus less likely to be out-competed as initial patch size increased.

Finally, planted species evenness may not have been affected by initial arrangement as effects of neighbors on the planted individuals may have been offset by local dispersal of their ramets into new locations. A species spatial strategy, the way individuals of a species use and occupy space, involves species responses to conspecific and heterospecific interactions and in their abilities to disperse into new locations (Bolker and Pacala 1999, Bolker et al. 2003). Some species (e.g. the clonal forb *M. fistulosa*) may routinely invest resources into dispersing into new locations via stolons or rhizomes. Such local dispersal would alter interactions that were established with the initial planting arrangements and may eliminate any effect of initial arrangement on species coexistence dynamics. In this study, planting arrangements were not maintained through time (Yurkonis unpub data) and it is plausible that local dispersal altered interactions among individuals as they were planted. Future studies need to investigate how local dispersal interacts with initial plant arrangement to affect species coexistence.

Our results support the hypothesis that larger-scale invasion increases with increasing heterogeneity at finer-scales (Davies et al. 2005, Melbourne et al. 2007). We found support for the hypothesis that invader abundance would be greatest in plots with fewer, larger patches. Early on, more light reached the soil surface and the light environment was more

heterogeneous in plots with initially larger patch sizes, suggesting that sites for establishment differed with different plant arrangements. This effect disappeared over time, likely because resident species or invaders spread into these locations and used this excess light. If invasion occurred in such areas with high light availability (Kennedy et al. 2002), then invader abundance should have been correlated with measures of the light environment, but this did not occur. Invasion was not greater in plots where the light environment was more heterogeneous or where there was more light available. This is counter to expectations that altering arrangements would produce more open spaces for colonization. Either we did not capture the light environment appropriately (e.g. the scale for measuring light was inappropriate) or invaders responded to more factors than light availability.

Invasion may have been related to the ease with which invaders dispersed through a plot once established (Bergelson et al. 1993, With 2002, 2004). Bergelson et al. (1993) assessed effects of gap size and arrangement on invasion and found that a grassland invader spread more readily when available gaps for establishment were larger and closer together. In our study, similar gaps, locations bordered by the same planted individuals, were more closely positioned in plots with larger initial patch sizes than in plots with smaller patch sizes (Figure 5.1). Thus, invasion may have increased with initial patch size as invaders could more readily disperse into new sites once established.

Regardless of the mechanism, our findings also have implications for how we view the effects of plant arrangement in managed communities. If seedlings are distributed in different ways as a community establishes (e.g. De Luis et al. 2008), then this pattern may affect future invasion. In this sense arranging plants in restored communities into fewer,

larger patches (Dickson and Busby 2009) may hinder restoration success because such arrangement may facilitate establishment of additional species.

Finally, this approach to quantifying effects of arrangement involved assessing plot-scale responses to initial patch size, a general metric describing plant arrangement. Initial patch size was correlated with the richness and the proportion of conspecific individuals surrounding any given individual. Initial patch size also likely describes the physical extent of patches of conspecific individuals (Yurkonis unpub data), which could affect local dispersal. Without specifically testing for associations of these factors (i.e., neighborhood richness, proportion of conspecific individuals, and ease of dispersal) with the response variables, it is unclear which aspects of plant arrangement affected the plot responses. Effects of planting arrangement on evenness may be better captured by quantifying plant arrangement through the association of species with one another or other neighborhood metrics (Chesson and Neuhauser 2002) and would provide a more mechanistic understanding of the effects of plant arrangement on plot-scale processes. Future studies of this nature need to focus on determining at what scales individuals interact (e.g., Vogt et al. 2010), the relative tolerance of conspecific and heterospecific interactions among the planted species, and what aspects of plant arrangement best capture changes in evenness (e.g., initial patch size versus probability of associating with conspecific individuals).

Conclusions

Connecting pattern and process in plant communities is challenging because in a multi-species community we cannot easily discern the degree to which individuals are affected by their neighbors. As a few studies have done (Stoll and Prati 2001, Idjadi and Karlson 2007, Hart and Marshall 2009), we approach this question concerning the relationship between

pattern and process in communities testing for the overall consequences of altering initial plant arrangement within a grassland community. In a perennial grassland system, it appears that initial plant arrangement may affect invasion resistance, but not planted species evenness. Future studies need to separate effects of arrangement on resident species dynamics from the effects on invasion resistance to assess if these findings are consistent in communities with less invasion pressure.

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CHAPTER 6. GENERAL CONCLUSIONS

A 1994 Special Feature in *Ecology* boldly declared space as “The Final Frontier for Ecological Theory”. In introducing the feature, Peter Kareiva indicated that experimental tests of predictions from models that consider how species use space when assessing species interactions are lacking and justified the feature as presenting general insights from such models to be taken up by empirical ecologists. With such an assertion, one would expect the feature to have led to a rapid and thorough investigation of the effects of pattern on process in plant communities, but this did not occur. Certainly, the most widely cited paper, Tilman’s contribution on competition-colonization tradeoffs (1994), sparked empirical studies (e.g. Turnbull et al. 1999), but it was soon clear that the theory could be refined further. Our theoretical understanding of the relationships between dispersal, competition, and environmental heterogeneity has expanded considerably since this publication (Pacala 1997, Silvertown and Wilson 2000, Bolker et al. 2003, Snyder and Chesson 2004, Hoopes et al. 2005). However, sixteen years later, only a few empirical studies have met Kareiva’s challenge (e.g. Stoll and Prati 2001, Idjadi and Karlson 2007, Hart and Marshall 2009), and, as the studies presented here indicate, much work still needs to be done.

To begin to empirically understand the links between pattern and process in perennial grassland communities, I considered factors that affect formation of plant pattern and effects of plant pattern in restored tallgrass prairie communities. In Chapters 2 and 3, I compared drill and broadcast seeded plantings and found that initial planting conditions affected subsequent plant pattern in these restored grasslands. Warm-season grasses were generally more abundant and occupied more space in drill seeded plantings. However, with such observational studies it is unclear if these differences arose from effects of seed arrangement

or depth of seeding in the plantings. I investigated this question in a subsequent greenhouse experiment and found that both depth and seed arrangement affected establishment, but in a surprising way. Unlike the established plantings, simulated drill seeded plantings were more diverse than broadcast seeded plantings (Figure 6.1a). Warm-season grasses were also less abundant in treatments where the seed was buried and were similar in abundance across drill and broadcast seeded treatments (Figure 6.1b). This result conflicts with field studies (Chapters 2 and 3) and suggests that differences in warm-season grass abundance between established drill and broadcast plantings arose from the ways warm-season grasses use space and compete with other plants after establishment. From a restoration standpoint, these findings suggest that traditional drill and broadcast seeding methods are interchangeable if

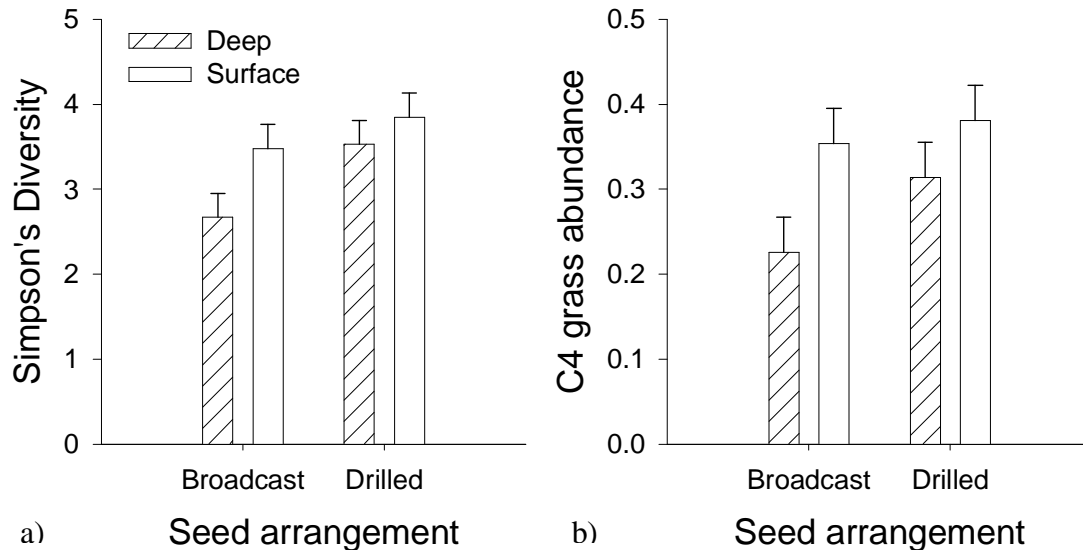


Figure 6.1 Mean Simpson's Diversity (a) and warm-season (C_4) grass abundance (b) when seeds were either hand broadcast or arranged in rows ("drilled") onto the ground surface or 1cm beneath the soil surface ("deep"). The most common planting methods are broadcasting seeds on the soil surface or drilling seeds 1 cm into the ground. Main effects of seed arrangement and depth of seeding are significant in (a) while only depth of seeding is significant in (b).

judging restoration success through the lens of species diversity, but not when considering other aspects of vegetation structure. From a more basic standpoint, these findings indicate that local density during establishment (i.e. seed arrangement) may have lasting effects on plant pattern, but more work needs to be done to determine in what ways this occurred and if such differences in plant pattern will result in future compositional differences between these types of plantings.

A second focus of the studies presented here was to investigate effects of plant pattern on communities. In Chapters 4 and 5, I demonstrate that invasion is linked to fine-scale plant arrangement, an effect that is potentially dependent on the identity of the resident species and independent of effects of plot-scale richness and evenness on invasion. In restored prairies, metrics describing fine-scale plant arrangement explained aspects of invader abundance that were not accounted for by larger-scale richness and evenness measures (Chapter 4). In this case, invader abundance was lower where native plants occurred in large patches. These plantings were dominated by cool-season grasses. When the cool-season grasses occurred in large patches, they may have inhibited establishment of typically cool-season invaders in this system by producing a thick litter layer (Bergelson 1990). In an experimental system, I found that invasion was linked to the initial planting arrangement. In this study, when plants were arranged into fewer, larger conspecific patches invader abundance was higher than when they were initially arranged into several, smaller patches (Chapter 5). Unlike the communities sampled in the observational study, the experimental communities contained a mixture of warm-season grasses and cool-season forbs. In this case, arranging plants into fewer, larger conspecific patches facilitated invader establishment. Both studies advance our understanding of the relationships between local diversity and invasion and provide novel

evidence that fine-scale heterogeneity affects invasion resistance in diverse perennial communities.

In an experiment designed to assess effects of initial pattern on species coexistence initial pattern and subsequent evenness were not related (Chapter 5), and future studies will focus on assessing the effects of pattern on species coexistence in grassland systems. Several factors may have affected this outcome. Arrangement may not have had an effect on evenness of the resident species because interactions between conspecifics and heterospecifics were similar, because local dispersal off-set changes in the competitive environment experienced by individuals with changing arrangement, or because pattern is more important at earlier stages (i.e. recruitment versus establishment phases). Effects of invaders on the resident individuals may have also outweighed effects of neighbors on one another in this study. The outcome may have been different in an otherwise similar study with less invasion pressure. This type of a study may be improved upon by assessing 1) effects of heterospecifics and conspecifics on individuals, 2) the relative scales of interactions among individuals (as in Vogt et al. 2010) at different life stages, 3) short and long distance dispersal within the resident species, and 4) effects of arrangement on coexistence with and without local invasion. With these types of data such an experiment may be better suited to test predictions from spatially explicit models of species coexistence (e.g. Bolker and Pacala 1999, Snyder and Chesson 2004).

Findings from these studies improve our understanding of the effects of initial plant pattern in communities, but care needs to be taken in extending such experimental findings to dynamics among individuals in established communities. Plant pattern in established communities is likely a product of initial conditions, local dispersal, interactions among

individuals, and individuals' interactions with the environment (Seabloom et al. 2005). Such pattern is dynamic, changing through time as local conditions change (Yarranton and Morrison 1974, Thorhallsdottir 1990, Herben et al. 1993, Yankelevich et al. 2006, Moore 2009) and is potentially further affected by legacies that plants leave on sites they once occupied (Casper et al. 2008). With the exception of Chapter 4, the studies presented here focused on effects of initial plant arrangement on subsequent pattern and process. I found that initial arrangement may lead to the formation of large, single species patches as seen in restorations (Allison 2002, Derner et al. 2004). I also found that arranging plants into initially large patches in restorations (as recommended in Dickson and Busby 2009) may not be advantageous in sites with high invasion pressure. However, it is still unclear if plant pattern in established communities may affect future dynamics in such communities. Future research projects will address if pattern in established vegetation affects subsequent dynamics and investigate the mechanisms underlying patch dynamics over time (as in Moore 2009).

Conclusions

It is challenging to connect pattern to process in plant communities and Kareiva's assertion that theory and experimental studies are not well connected is certainly still valid. In considering effects of pattern in established communities, we need to understand what factors contribute to pattern formation, and in what ways present pattern may affect future dynamics. I began to study these links in tallgrass prairies by considering scenarios where initial plant pattern was altered (either through density or arrangement of conspecific individuals) and competition among individuals, local dispersal, and invasion were allowed to proceed. In this approach to understanding effects of plant pattern on process, I provide a much needed

comparison of common restoration methods and investigate if altering initial plant arrangement affects restoration success. Initial arrangement affected the communities that developed within these studies in various ways and I determined that two common restoration methods are interchangeable when assessing restoration success through the lens of species diversity. Moving forward with this research, I plan to test the mechanisms underlying these responses and further investigate if restoration success may be improved by altering initial plant arrangement.

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