INVASION OF SMOOTH BROME INTO NORTH AMERICAN TALL-GRASS PRAIRIES: IMPACT ON NATIVE PLANT/HERBIVORE SPECIES AND MECHANISMS RESPONSIBLE FOR SUCCESSFUL INVASION

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ABSTRACT

Research in invasion ecology has focused on developing ecological theory that can predict how invasive species interact with invaded communities. However, empirical support for theoretical predictions has been inconsistent. Inconsistencies may be attributed to the lack of data in three core areas; (1) field data with enough resolution to determine population dynamics of invasive species in relation to native species, (2) manipulative field experiments that encapsulate natural variation found among micro-habitats, and (3) field data that incorporates effects of invasive species within and among spatial scales. This dissertation has addressed these concerns by examining the mechanisms responsible for the successful invasion and ecological impacts of the invasive grass smooth brome (*Bromus inermis*) within the prairies of North Dakota and Minnesota. GIS analyses revealed that native *Spartina pectinata* (cordgrass) patch growth was two times greater in non-invaded areas versus areas heavily invaded with brome. The probability of extinction of native *Spartina pectinata* averaged 8 times more likely in areas of high versus low brome coverage. Field experiments determined differences in germination between invasive smooth brome and native prairie cordgrass were not driven by habitat differences or soil conditions. Following initial germination, invasive smooth brome had a negative impact on cordgrass establishment, which was primarily due to a 78% and 47% reduction in native cordgrass plant height and stems density, respectively. Throughout the field experiment invasive smooth brome was a dominant competitor under all habitats and soil conditions except in areas where soil salinity levels were highest. Results from an herbivore study indicated that smooth brome has the potential to have negative effects on local herbivore assemblages. Despite the large differences in herbivore species richness, diversity and evenness at larger spatial scales, results indicated no statistically significant effects of invasive smooth brome. Results indicated that plant species richness had a larger effect than invasive smooth brome on herbivore assemblages. This dissertation provides support indicating that the invasion of smooth brome into native prairie remnants is detrimental to many native species present in tallgrass prairie fragments and that intensive management practices are needed to prevent future spread across the prairie landscape.

CHAPTER 1. INTRODUCTION

Research in invasion ecology has focused on developing sound ecological theory that can predict how invasive species alter key ecological processes (e.g. nutrient cycling, plant productivity, native plant assemblages etc.; Mack et al. 2000) and in turn how those changes can affect native food web composition (e.g. abundance of organisms, predator/prey relationships and herbivore community assemblages). Considering the impact that invasive plants can have on native communities, land managers and researchers have emphasized the importance of identifying mechanisms that contribute to the successful invasion of non-native plants and their impacts on native communities (Parker et al. 1999, Shea and Chesson 2002).

In this dissertation, I tested the hypotheses that invasive species have the ability to suppress the growth and persistence of native species through high seed germination (Levine 2000) and competitive ability (Callaway and Aschehoug 2000). I also tested the hypothesis that once established, invasive plants have the ability to alter local herbivore species richness, diversity and evenness. I used the invasive grass smooth brome (*Bromus inermis*) as a model organism to help explain patterns observed in species interactions between smooth brome and prairie cordgrass (*Spartina pectinata*), a dominant native prairie plant associated with the tallgrass prairies of the Midwestern United States . I also examined how smooth brome interacts with the herbivore assemblage associated in these prairie systems.

Smooth brome was originally introduced into North America in the late 1880’s from Hungary and Russia (Hitchcock 1963) and has established by invading disturbed prairies (D’Antonio et al., 1992), as well as through repeated anthropogenic introductions to help provide soil retention and animal graze (Larson et al. 2001). Following its introduction, smooth brome has dispersed from its originally planted areas and established in native prairie fragments

(D'Antonio and Vitousek 1992). Compared to its close relative, cheatgrass (*Bromus tectorum*), a highly noxious weed (USDA and NRCS 2010), smooth brome has been largely ignored as an invasive species, possibly due to its economic value as a forage plant (NISC 2006). To date, there is very little experimental data regarding the factors that contribute to its invasiveness (but see Otfinowski and Kenkel 2008, Otfinowski et al. 2010) or its impacts on native communities (but see Haynes and Cronin 2003; Cronin 2003, Baum et al. 2004, Cronin and Haynes 2004, Cronin et al. 2004, Cronin 2007).

In Chapter 2, I examined the impact of smooth brome on the patch dynamics of a native dominant species *Spartina pectinata*. I used a fine scale (sub-meter) GIS spatial analysis to characterize some of the population dynamics concerning native prairie cordgrass in relation to the abundance of established smooth brome. This research was conducted across three prairie fragments from 2000-2006 to help determine if smooth brome was capable of displacing native prairie cordgrass in its native habitat. I hypothesized that as the abundance of smooth brome increased it would negatively affect the growth, persistence, colonization and extinction of native prairie cordgrass patches.

In Chapter 3, I conducted a field experiment to determine if invasive smooth brome and native cordgrass were capable of germinating and surviving when grown alone or in the presence of one another in dominant habitats across the landscape. I used these data to determine how germination success and potential competitive ability could help explain major patterns found in the observational study from Chapter 2. Currently there is no clear understanding of what mechanisms allow for the spread of smooth brome into native prairie fragments. It is possible that smooth brome is a superior competitor and is simply outcompeting cordgrass for resources. It was also possible that other factors were causing the decline of cordgrass and acting independently of the spread of brome. Understanding what mechanisms are influencing the spread of brome and the decline of cordgrass is critical if we want to develop a plan for eradicating or limiting the distribution of brome across the prairie pothole region. The experiment was performed across the range of habitat types that dominate the prairie landscape. These habitat types were (1) mono-specific stands of the dominant native prairie cordgrass (*Spartina pectinata*) (Hitchcock 1963), (2) mono-specific stands of established invasive smooth brome (*B. inermis*), (3) mudflats, which are slightly lower in elevation and mostly consist of bare ground and saltwort (*Salicornia rubra*) in dry periods, and are covered by water in wet periods and (4) mixed native habitat, which is a mixture of native grasses with no clear dominant species (Cronin and Haynes 2004). In this experiment, I also characterized soil conditions (elevation, moisture, salinity, pH and % nitrogen) that naturally occur across the four habitat types to help determine what role they may have in the successful colonization and establishment of smooth brome.

In Chapter 4, I conducted a multi-scale study ranging from 1-m^2 plots, to prairie fragments, to watersheds to determine if the relative abundance of smooth brome was correlated with herbivore community assemblage richness, diversity and evenness. Field sites varied in the abundance of smooth brome allowing me to test the prediction that as the abundance of smooth brome increased across spatial scales, herbivore species richness and diversity would decrease. Herbivore evenness was calculated to determine if there was any relationship with smooth brome abundance. This research was the first study to examine how herbivore community assemblages change as the abundance of smooth brome increases at large (landscape and regional scale) spatial scales.

In Chapter 5, I summarized the main findings of the GIS survey, field germination/competition experiment and multi-scale herbivore survey. Finally, I discuss how my research contributes to current invasion biology theory to help justify the current management practices for smooth brome across the tallgrass prairies.

CHAPTER 2. PATCH DYNAMICS OF A NATIVE GRASS IN RELATION TO THE SPREAD OF INVASIVE SMOOTH BROME (*BROMUS INERMIS*)[1]

Introduction

Over the past 200 years, the number of non-native species within a community has increased precipitously due to human migration and commerce (Hodkinson and Thompson 1997; Kowarik 2003; Mack et al. 2000; Mooney et al. 1986; Vitousek 1997). Invasive plants pose significant threats to native communities by altering ecosystems processes (Vitousek and Walker 1989; Dyer and Rice 1999; Bart and Hartman 2000; Mack et al. 2001; Ehrenfeld 2003), biodiversity levels (Brown and Gurevitch 2004) and community structure (García-Robledo and Murcia 2005; Gratton and Denno 2005). Moreover, invasive species are considered one of the top two factors (along with habitat loss/fragmentation) influencing extinction risk of native species (Wilcove et al. 1998; Clavero and Garcia-Berthou 2005). To understand the invasion process and the impact that invasive species have on native species, it is of paramount importance to develop programs that monitor the spread of invasive species and the associated changes in the distributional patterns of native species over time (Stohlgren et al. 1998; Thomson 2005).

Classic reaction-diffusion theory predicts the smooth and gradual spread of invasive organisms into novel habitats (Fisher 1937; Skellam 1951), and large, regional-scale distributional studies tend to support this notion (reviewed in Hengeveld 1989). However, when examined at finer spatial scales (e.g., within a forest stand or grassland fragment), invaded habitats are often heterogeneous and characterized by a mosaic of small and isolated local populations (or patches) of the invasive and native species (for example, see Johnson et al.

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2006). At this smaller scale, the spatial and temporal distribution of patches of native and invasive species may be quite dynamic (Chabrerie et al 2007) and the complete displacement of native species may never occur (Sax et al. 2002). It is at this scale that native-invasive interactions take place (Gurevitch et al. 2002; Theoharides and Dukes 2007). Fine-scale (sub-meter) monitoring programs may be necessary for the detection of the effects of invasive species on the patch dynamics (growth, local extinction and establishment) of native species (e.g., Barbraud et al. 2003; Bradley and Mustard 2006; Prather et al. 2005).

Remote sensing has become a popular and valuable tool for monitoring the spread of invasive plant species, and associated changes in the distribution of native flora (Pengra et al. 2007). The advantages of remote sensing are well known and include the collection of data that span broad spatial and temporal scales. However, the usefulness of remote sensing is limited by the accessibility of data for certain regions, coarse resolution of data (e.g., 30 m^2 pixel size with LandSat Thematic Mapper data; Madden 2004; Mladinich et al 2006), and prohibitive costs associated with multi or hyperspectral data that are necessary to differentiate plant species.

Ground-based approaches that use traditional surveying equipment or global positioning systems (GPS) are time consuming and labor intensive (Everitt et al. 1992), but have distinct advantages over remote sensing. Most notably, ground surveys can resolve fine-scale distributional patterns of species (< 1 m) - the scale at which species interactions are likely to be strongest (e.g., interspecific competition; Gurevitch et al. 2002). Moreover, structurally or spectrally similar species may be indistinguishable with available remote sensing data and can only be separated by competent botanists in the field. Finally, the patterns of establishment and extinction of native and invasive plant patches can be discerned with traditional ground surveys. For example, by mapping and monitoring the spread of the invasive perennial herb, *Hieracium* *lepidulum*, Wiser et al (1998) were able to determine that the invasion patterns were related to dispersal limitation, community structure, disturbance history and environmental characteristics.

In this study, we employ a fine scale (sub-meter) GPS survey spanning six-years to quantify the change in distributional patterns of invasive smooth brome (*Bromus inermis* Leyss) and a dominant native grass (prairie cordgrass, *Spartina pectinata* Link) within tall-grass prairie fragments of eastern North Dakota. Currently, no information is available on the spread of smooth brome at large or small spatial scales, or on how temporal changes in the distribution of smooth brome affect the distribution of native plant species. Our survey involved mapping the distribution of all clonal patches of brome and cordgrass in three prairie fragments from 2000 to 2006. Specific objectives of this survey included determining 1) the change in habitat coverage of prairie cordgrass over time, 2) whether the growth of cordgrass patches were correlated with the proportion of smooth brome adjacent to those patches, and 3) whether the extinction of existing cordgrass patches or establishment of new cordgrass patches was related to the prevalence of brome in the surrounding area.

Methods

Invasive Smooth Brome

In North America, the vast majority of native prairie habitat has been converted into agricultural land (Stoner and Joern 2004). Consequently, prairies are one of the most imperiled ecosystems in the world (Stoner and Joern 2004). To date, native mixed prairie habitat has been reduced by approximately 70% (Samson et al. 2004) with the remaining prairie fragments supporting up to 50 invasive species, roughly 12.5% of all plant species present (North Dakota Department of Agriculture 2008), many of which were intentionally introduced into the region for agricultural purposes (Mack et al. 2000; Weston and Duke 2003; Seabloom et al. 2006).

Smooth brome was originally introduced into North America in the late 1880's from Hungary and Russia (Hitchcock 1963) for soil retention and to provide animal graze (Larson et al. 2001). More recently, brome has escaped from its planted habitats and become established in native remnant prairies (D'Antonio et al. 1992). At present, smooth brome has received little attention as an invasive species (but see Blankespoor and Larson 1994), despite the fact that its invasive status has been often noted (Haynes and Cronin 2003; Cronin and Haynes 2004; Otfinowski 2007; Williams and Crone 2006; Cronin 2007). For instance, Williams and Crone (2006) developed a demographic model based on natural patches that indicated smooth brome is capable of slowing the growth and promoting the extinction of native *Anemone patens* (Pasque flower) patches. Similarly, in a greenhouse study, brome has been shown to maintain a high competitive ability under a variety of abiotic conditions (Nernberg and Dale 1997). At the community level, smooth brome can alter native plant diversity and increase homogenization of native habitats (Oftinowski et al. 2007). Finally, several authors have demonstrated that brome significantly impacts the movement behavior and population dynamics of several native arthropod species (Haynes and Cronin 2003; Baum et al. 2004; Cronin 2003*ab*; Cronin and Haynes 2004; Cronin et al. 2004; Cronin 2007). For example, smooth brome promotes high rates of dispersal of a planthopper (*Prokelisia crocea*) and its parasitoid (*Anagrus columbi*) among patches of prairie cordgrass, and that this results in local and regional extinction of their populations (Cronin & Haynes 2004; Cronin 2007).

Study System

Our study was conducted in Kelly's Slough National Wildlife Refuge in Grand Forks County, North Dakota (47.941848 N, 97.310368W). Kelly's Slough was developed to establish and manage wetlands and grasslands unique to the Red River Valley (USFWS 2008). Within this refuge, there are approximately 355 ha of protected habitat with the upland areas comprised primarily of grasslands. A dominant native grass species in these prairie fragments is prairie cordgrass (Hitchcock 1963). Cordgrass grows clonally and forms discrete patches that range in size from a few stems to over 4 ha (Cronin 2003a). Most other native grass species grow in very diffuse patterns with no clear dominant species present. These species include foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb. and little bluestem *Andropogon scoparius* Michx. These prairie fragments also contain mudflats, which are slightly lower in elevation and mostly consist of bare ground and saltwort (*Salicornia rubra* Nels.) in dry periods, and are covered by water in wet periods.

Smooth brome was likely introduced into Kelly's Slough around the early to mid 1900's (K Tompkins, Refuge Manager, Kelly's Slough National Wildlife Refuge, personal communication) and to date, expansive monocultures of smooth brome occupy the prairie (Cronin 2003*a*; Haynes and Cronin 2003). Currently, the United States Fish and Wildlife Service employs a broad spectrum management plan within the Kelly's Slough refuge system to reduce abundances of a variety of woody and invasive species (Emery and Gross 2005; Simmons et al. 2007; K Tompkins personal communication). Management involves a combination of prescribed burns, tillage, haying, grazing and chemical treatments.

Vegetation Mapping

The position and perimeters of all cordgrass patches (≥ 0.25 m^2) were mapped in three different field sites within the Kelly's Slough drainage system (Site 104, LimeHouse, and North Kelly's). Field sites ranged in size from 36-55 ha (Table 1). Mapping was conducted at three different time-periods (June of 2000 and 2004 and July of 2006) using either a Leica Geosystems 500 (with Coast Guard beacon receiver) or a Trimble GeoXT (WAAS enabled) system. Both

Table 2.1: Summary statistics for the three field sites, Site 104, LimeHouse and North Kelly. Data are divided among 3 time periods (2000, 2004, and 2006).

Prairie fragment	Area (ha)	2000		2004			2006		
		Cordgrass coverage (%)	Cordgrass patches (N)	Cordgrass coverage (%)	Brome coverage (%)	Cordgrass patches (N)	Cordgrass coverage (%)	Brome coverage (%)	Cordgrass patches (N)
Site 104	46	17	704	12	10	282	16	12	647
Limehouse	36	19	274	18	27	162	19	30	280
North Kelly	33	27	340	24	27	139	25	26	228
Mean ± 2 SE	45.7 ± 2.06	21 ± 1.53	439 ± 10.14	18 ± 1.63	21.3 ± 2.09	194.3 ± 5.84	20 ± 1.43	22.7 ± 2.05	385 ± 10.07

systems had a < ¾ m^2 margin of error. For patches of cordgrass to be considered distinct from one another, they had to be separated > 0.5 m (Cronin 2003a, b, and c). Smooth brome was only mapped in the latter two census periods. For both plant species, we used a GPS unit set to record positions at 1-second intervals, and walked the perimeter of every patch within a site. For each cordgrass patch in 2004 and 2006, we also quantified the proportion of the habitat within a 1-m buffer area that was composed of brome. These data were used to determine if the amount of neighboring brome was correlated with the growth rates of cordgrass patches. We chose a distance of 1 m because smooth brome and prairie cordgrass are capable of spreading by this distance during a single growing season (Otfinowski 2007; USDA and NRCS 2008). Therefore, competitive interactions are likely to take place within this buffer area. We used the following proportional categories to characterize the amount of brome within this buffer area: 1) <25%, 2) 25% to 50%, 3) 50% to 75%, and 4) 75% to 100%.

We imported prairie cordgrass and smooth brome positional data into ESRI ® ArcMap ™ 9.0. A separate database was created for each field site, and each plant species - year combination was treated as a separate theme (or layer) (Fig. 2.1). Patches that broadly overlapped between years were considered to be the same patch. We used the ArcMap Extension, XTools Pro v. 2.2 (Delaune and Chikinev 2005), to calculate the area of each field site and each patch of smooth brome and cordgrass. To calculate the percent coverage of each plant species within a field site, we summed patch areas and then divided this sum by the total area of the site.

Temporal trends in patch size were evaluated with a repeated-measure ANOVA. Site was a fixed factor and patch size at different census periods was the repeated measure. The purpose of the test was to assess whether changes in mean patch size over time differed among the three

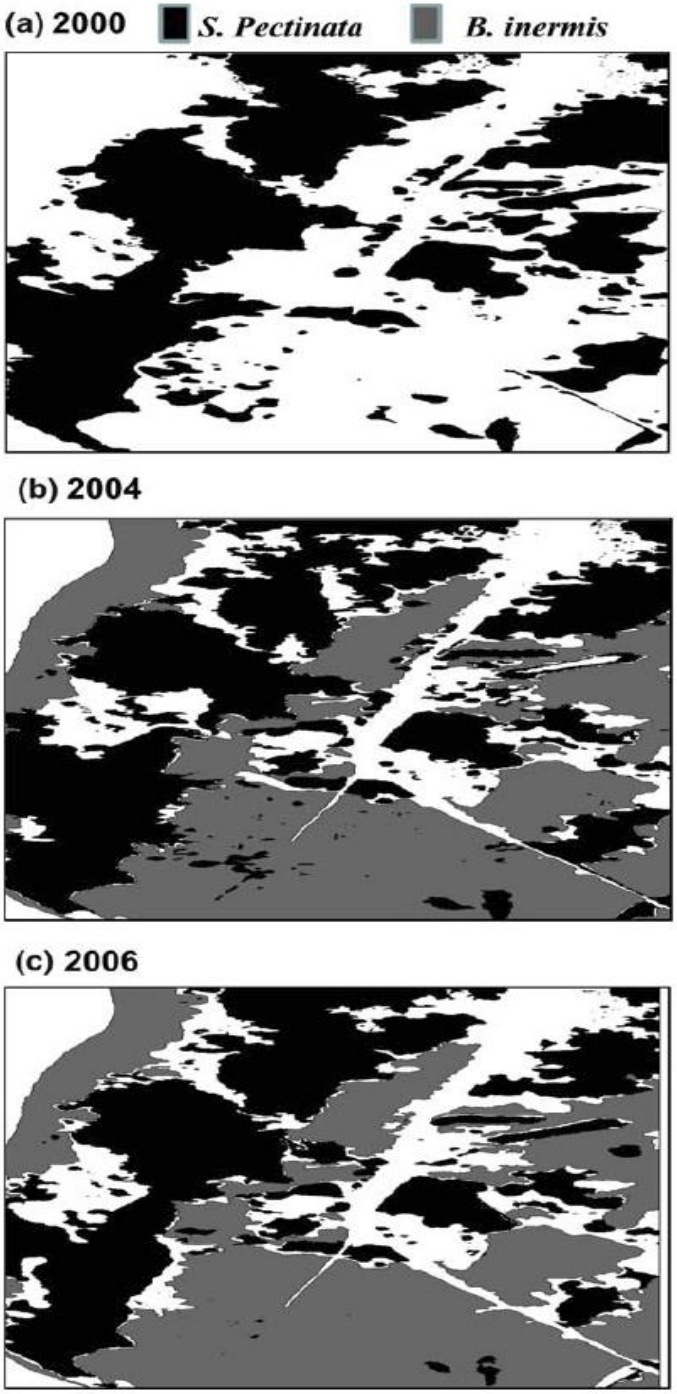


Fig. 2.1: The spatial distribution of cordgrass and brome Patches in a portion of the field site North Kelly's (a) cordgrass patches in 2000, (b) cordgrass and brome in 2004, and (c) cordgrass and brome in 2006. Brome distribution was not mapped in 2000 and is therefore unknown.

prairie sites (a significant time*site interaction). Following a significant time effect, differences between any two-time periods were assessed with separate paired t-tests. To guard against inflated type I errors associated with three different tests, a sequential Bonferroni correction was used to assess significance.

To determine how the establishment of brome influenced the growth of cordgrass patches, we computed the annual rate of change in area for each patch *i* for the time-periods 2000 - 2004, 2004 - 2006, and 2000 - 2006. Here, the annual rate of change in size of patch *i* equals A_{i+1}/A_i divided by the number of years between surveys. *A* is patch area in m^2. This growth rate scales from zero (e.g. patch extinction) to infinity. No growth rate was computed for patches that were

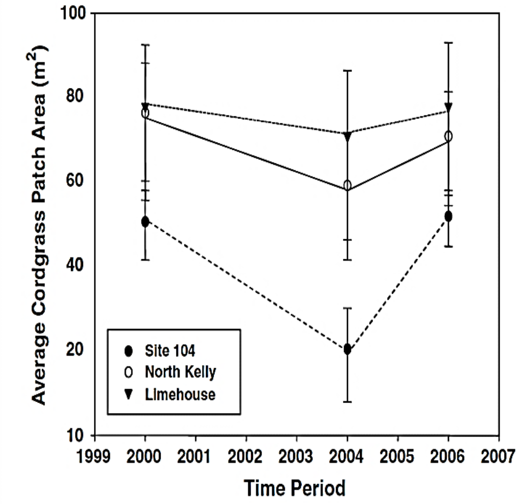


Figure 2.2: The mean ± SE cordgrass patch size (m2) for each time period measured. Separate symbols were used for each field site.

absent at the start of the time-period. The distribution of growth rates was strongly right-skewed. Therefore, we employed a non-parametric Kruskall-Wallis test to determine whether cordgrass growth rate (dependent variable) was related to the percent brome (<25%, 25% to 50%, 50% to 75%, and 75% to 100%) adjacent to the patch (independent variable). A sequential Bonferroni correction was used to adjust for potentially inflated type I errors associated with multiple non-independent tests (i.e., the three time periods within a site). Differences between categories of brome were assessed with non-parametric Mann-Whitney U tests.

Establishment and Extinction of Cordgrass Patches

We tested the hypothesis that the establishment of new cordgrass patches and the extinction of existing patches between time-periods were significantly related to the proportional coverage of brome immediately surrounding the patch. We determined the number of cordgrass patches per brome-coverage category that remained extant between time-periods (e.g., patch that was present in 2000 and 2006), were newly established (e.g., patch not present in 2000 but present in 2006) and went extinct (e.g., patches present in 2000 but not 2006). Separate chi-square tests for independence were performed to determine if cordgrass establishment and extinction likelihood differed significantly between areas differing in brome coverage. Data from all three-field sites were combined into patches that had <50% or > 50% brome surrounding a patch of cordgrass. This procedure ensured that sample sizes per brome and extinction/establishment categories were sufficient to perform the chi-square tests (*n* > 5 per category). We predicted that cordgrass extinctions would be more common and establishments would be less common in brome-dominated areas. Because extinction rates were expected to be greater for small, as compared to large, cordgrass patches, we also tested whether cordgrass patch size was confounded with brome coverage. Differences in patch size between areas of high and low brome coverage were evaluated with a paired *t*-test for each time-period. We used an *ln* transformation on patch area for each period in order to meet assumptions of normality.

Results

Mean patch size varied among years (F=8.482, df =2 and p<0.001) (Fig. 2.2) and did not vary across sites (F=1.016, df=2 and p>0.36). There was no significant time*site interaction (F= 2.360, df= 4 and p>0.05). From 2000-2004, mean cordgrass patch size declined by an average of 16 % (- 27.4 m^2 ± 14.701, p-value <0.001) across all three field sites, whereas from 2004-2006, cordgrass patches significantly increased in size by 12% (19.577 m^2 ± 8.5276, p-value < 0.001). Consequently, there was no significant net change in cordgrass patch size over the six years of this study (p-value < 0.791) (Fig. 2.2).

The growth rate of cordgrass patches was significantly affected by the proportion of smooth brome adjacent to the patch in all but one of the 9 possible tests (three sites and times three time periods; Table 2.2). In general, growth rates declined as the proportion of brome increased (Fig. 2.3). For example, from 2000-2006, cordgrass patch growth was approximately 2 times greater for patches with < 25% versus patches with 75%-100% brome surrounding the patch (χ^2=24.93, df = 2, and p<0.001).

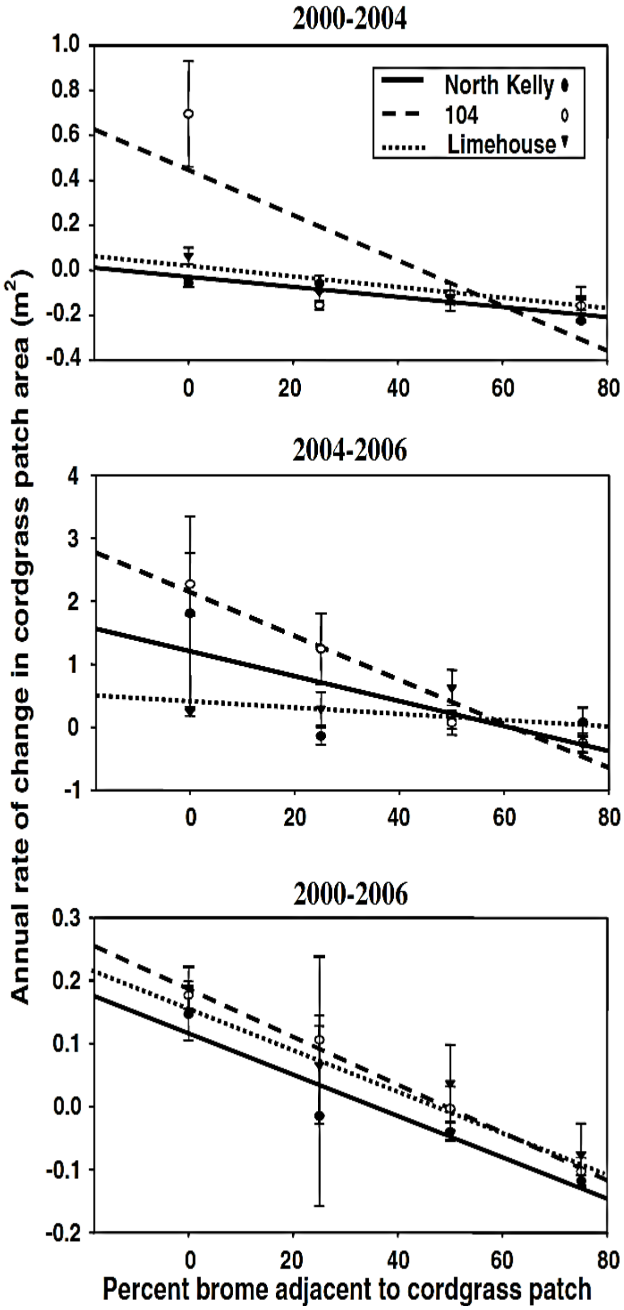


Figure 2.3: The mean ± SE percent change in cordgrass patch size (see Methods) in relation to the percentage of brome within a 0.5 m buffer surrounding the cordgrass patch. For each site, the change in patch size is reported for three different time periods. The lines were fit by least-squares regression and are only intended to reveal trends in the data.

Table 2.2: Results from separate Kruskall–Wallis tests for the effect of percent brome surrounding a cordgrass patch (<25%, 25–50%, 50–75%, and >75%) on the percent change in cordgrass area.

North Kelly	2000–2004	4	100.007	<0.001
	2004–2006	4	13.788	<0.027
	2000–2006	4	85.153	<0.001
Site 104	2000–2004	4	21.601	<0.001
	2004–2006	4	60.595	<0.001
	2000–2006	4	135.095	<0.001
Limehouse	2000–2004	4	16.183	<0.009
	2004–2006	4	11.260	<0.090
	2000–2006	4	29.150	<0.047

Bonferroni-adjusted P-values are reported and account for potentially inflated type I errors associated with multiple tests per field site.

New cordgrass patches were 1.5 (2000 - 2004: χ^2 =16.253, p < 0.001), 1.2 (2004-2006: χ^2=4.975, p<0.036) and 1.3 (2000-2006: χ^2= 5.43, p<0.020) times more likely to become established in areas consisting of <50% brome than areas of ≥ 50% brome (Fig. 3.4). Similarly, cordgrass patch extinctions were very strongly affected by brome coverage. Extinction of cordgrass patches was 1.4 (2000-2004;

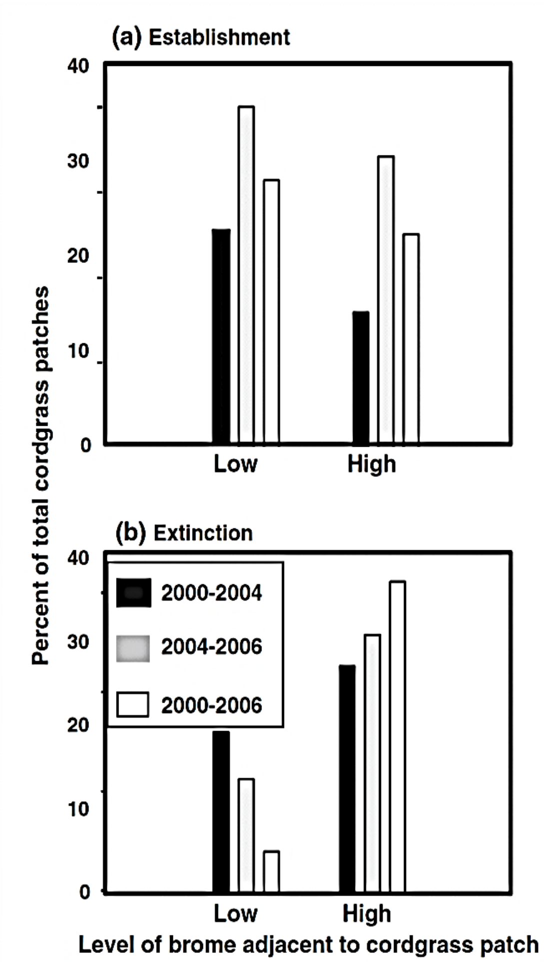


Figure 2.4. Percentage of cordgrass patches that (a) became established or (b) went extinct in habitats consisting of a low (<50%) or high (>50%) percentage of brome. Separate bars are used for each time period.

χ^2=13.487, p>0.001), 2.3 (2004-2006; χ^2=37.542, p<0.001) and 7.8 (2000-2006; χ^2=237.92, p<0.001) times more likely in areas ≥ 50% relative to areas < 50% brome coverage (Fig. 3.4). The cause for the relatively high extinction risk of cordgrass patches in brome-dominated areas is not a consequence of smaller cordgrass patches being associated with high areas of brome. In fact, we found the opposite pattern. Mean cordgrass patch size was greater in areas of high versus low brome for every time-period (mean difference in 2000 = 1.494 m^2, df=167, t= 10.123 p<0.001; mean difference in 2004 = 0.862 m^2, df=95, t=2.343, p<0.001; and mean difference in 2006 =1.243 m^2, df=95, t=4.11, p<0.001).

Discussion

Our study provides rare data on the establishment, growth and extinction of native plant patches in relation to the spread of an invasive plant species (for other exceptions see Huang et al. 2007; Rice et al. 2000). It also reveals consistently strong support for the hypothesis that invasive smooth brome is detrimental to the patch dynamics of prairie cordgrass. Not only are the growth rates of established cordgrass patches negatively related to the proportion of brome in the matrix surrounding each patch, but also areas dominated by brome (≥ 50% coverage) are approximately 1.3 times less likely to be colonized by cordgrass and 8 times more likely to have a cordgrass patch go extinct. Although our data are only correlative, we suggest that brome has a direct negative effect on cordgrass abundance. This conclusion is corroborated by the recent experimental work of Williams and Crone (2006) who demonstrated that smooth brome was capable of lowering survivorship and slowing the growth of native *Anemone patens*, a long-lived native perennial of North American grasslands. Furthermore, F. P. Dillemuth et al. (unpublished data) transplanted cordgrass seeds and seedlings into brome and cordgrass dominated habitats and found that growth rates and survivorship were lowest in brome. Our survey results, in combination with these experimental studies, support a large body of literature that invasive plants are able to reduce abundances of native species in infested habitats (e.g., Keane and Crawly 2004; Mack et al. 2000).

Despite the negative association between brome occurrence and cordgrass patch dynamics, it is not clear that brome would eventually displace cordgrass in our study sites. From 2000-2004, cordgrass patches declined in size by an average 27 m^2 (16%), but between 2004 and 2006, cordgrass patches increased in size by 20 m^2 (12%) resulting in no net change in cordgrass patch size from 2000-2006. The decline in the first time period cannot be attributed solely to smooth brome because cordgrass patch sizes decreased in areas of high and low brome coverage (although, it was greater for the former areas; see Fig. 2.2). The difference in cordgrass growth rates between 2000-2004 and 2004-2006 may be due to changes in precipitation levels. In 2000-2004, precipitation levels averaged 7% above the hundred-year norm for the May-August growing season (National Climatic Data Center 2007). The period 2004-2005 was particularly wet and had precipitation levels 22% above the above the hundred year average. These heavy rains resulted in standing water across all of our field sites for much of the growing season. Cordgrass is more hydrophytic than most prairie plants (Sedivec and Barker 1998) and likely thrived under these conditions. The effects of this unusually wet period on cordgrass probably extended through the end of our study period.

Another reason why brome may not displace cordgrass is because of microhabitat differences in performance of both species. Although these prairie fragments are quite flat (< 0.5 m elevational change), relatively low areas may favor cordgrass over brome. Our transplant experiment F. P. Dillemuth et al. (unpublished data) supports this assertion. Brome seedling transplants did poorer than cordgrass in low areas dominated by cordgrass, even when potential competition from cordgrass was removed. Given the spatial and temporal heterogeneity observed in these prairie habitats, the complete displacement of cordgrass by brome (at the scale of a prairie fragment) probably would require either an extended drought period, or the accretion of sediments by brome and the gradual elimination of low spots in the prairie. Our conclusion that invasive smooth brome is unlikely to cause the extinction of native prairie cordgrass is consistent with the current paradigm regarding invasive exotic species (Sax et al. 2002; Tilman 1997). For example, New Zealand has over 2069 known successful exotic colonizers but only 3 known extinctions of native plants (Sax et al. 2005).

Through its effects on cordgrass patch growth and extinction-establishment dynamics, brome can have important consequences for cordgrass population dynamics. Once brome has gained a foothold in a habitat, it may represent a barrier to the spread of cordgrass (see Standish et al. 2001). If for example, dry conditions favor the spread of brome (Blankespoor and Larson 1994) into cordgrass habitat, it may be difficult for cordgrass to spread back into its old habitat after wet (favorable) conditions return (Wilson et al. 2004). Also, as brome spreads across the prairie landscape it may fragment or cause the extinction of local stands of cordgrass and increase isolation among existing patches (Cronin 2007; Cronin and Haynes 2004; Haynes and

Cronin 2006; Haynes et al. 2007). Isolation of cordgrass patches, coupled with a reduction in patch size, may increase the likelihood of inbreeding and strengthen Allee effects associated with small population size (Davis et al. 2004 a, b).

Brome invasion is also likely to have effects that extend to higher trophic levels. For example, Cronin and his colleagues (Haynes & Cronin 2003, 2006, Cronin 2003, 2004, 2007; Cronin, Haynes and Dillemuth 2004) have explored the consequences of the invasion of smooth brome on the primary herbivore of cordgrass, the planthopper *Prokelisia crocea*, and the planthoppers specialist natural enemy, the parasitoid *Anagrus columbi*. Movement studies have revealed that planthoppers and parasitoids are more likely to emigrate from cordgrass patches embedded in a brome matrix than in native matrix habitat (Haynes and Cronin 2003, 2006; Baum et al. 2004; Cronin and Haynes 2004). Because of brome’s effect on emigration behavior, local populations of *P. crocea* and *A. columbi* are reduced in density by 50% and are 4-5 times more likely to go extinct than in patches surrounded by native vegetation (Cronin and Haynes 2004). Moreover, at the landscape level, brome dominated landscapes can lead to the extinction of planthopper and parasitoid populations (Cronin 2007). As was recently demonstrated by Cronin (2007), by infiltrating cordgrass patches and diminishing patch area, brome may degrade cordgrass patch quality to the extent that patches pass from population sources to sieves and eventually to sinks. Finally, the parasitoid is far more sensitive than its host to the invasion of brome (with regard to all of the above parameters) (Cronin and Haynes 2004, Cronin 2007). This one detailed case study highlights the potential consequences that invasive plants may have on the remainder of community. Bottom-up effects, owing to invasive plant species, have been reported for other systems and reflect the complex direct and indirect interactions that may occur during the invasion process (Ellingson and Anderson 2002; Gerber et al. 2008; Gratton and Denno 2005).

Brome Management

Based on the available data with smooth brome (this study; Blankespoor and Larson 1994; Murphy and Grant 2005; Willson and Stubbendieck 2000), the lack of a management plan can have dire consequences for dominant prairie plants (F. P. Dillemuth unpublished data), and potentially many native arthropod species. Currently, management of smooth brome is limited because other invasive species (e.g. *Cirsium arvense*, Canada thistle; *Euphorbia esula*, leafy spurge and *Artemisia absinthium*, wormwood) have been given higher priority by local land managers (K. Tompkins, personal communication). However, land managers report some success in reducing the establishment, spread and abundance of smooth brome with the use of prescribed burns (Wilson and Stubbendieck 2000). This type of management has been successful in previous habitats dominated by Spartina dominated habitats (see Feldman 2004; Schmalzer 1991). The basis for this management tactic is a model developed by Willson and Stubbendieck (2000) that recommends burning in early spring at the four or five leaf stage of smooth brome. This tactic is thought to work because smooth brome is a cool season grass that begins its growth cycle and sets seeds before native warm season grasses (i.e. prairie cordgrass). Therefore, a properly timed prescribed fire may reduce smooth brome abundance before it set seeds, while freeing up space and resources for native warm season grasses to flourish. According to Willson and Stubbendieck (2000), warm season grasses needed to respond and achieve a minimum of 20% coverage before the next year’s growth cycle begins for this practice to effectively reduce smooth brome populations. Rigorous field-testing of this management tactic has yet to be attempted. If fire is not an option, then land managers may have to rely on mechanical methods (tillage which may have to be repeated over several years), haying, grazing or chemical treatment (Tompkins Personal communications 2008). Unfortunately, these latter approaches are likely to be more expensive and less ecologically sound than burning.

CHAPTER 3. SEEDLING EMERGENCE AND INTERSPECIFIC COMPETITION OF AN INVASIVE SPECIES IN THE TALLGRASS PRAIRIES OF NORTH AMERICA

Introduction

Over the last two centuries, human migration and commerce have led to a dramatic increase in the number of non-native species introductions across the globe (Mooney et al. 1986, Hodkinson and Thompson 1997, Vitousek 1997, Mack et al. 2000, Kowarik 2003). Invasive plants are of particular concern because they pose significant threats to invaded communities by altering ecosystem processes (Vitousek and Walker 1989, Dyer and Rice 1999, Bart and Hartman 2000, Mack et al. 2001, Ehrenfeld 2003), biodiversity levels (Brown and Gurevitch 2004), interactions among trophic levels (Cronin and Haynes 2004, Wolkovich et al. 2009) and community structure (García-Robledo and Murcia 2005, Gratton and Denno 2005). Moreover, invasive species are considered one of the top two factors (along with habitat loss and fragmentation) influencing extinction risk of native species (Wilcove et al. 1998, Clavero and Garcia-Berthou 2005).

Given the impact that invasive species can have on invaded communities, researchers and land managers have attempted to identify critical mechanisms that contribute to the successful invasion of non-native plants and their impacts on native communities (Parker et al. 1999, Shea and Chesson 2002, Ziska et al. 2011). Interspecific competition (Crawley 1990, Mangla et al. 2011) and germination success (Grime et al. 1988, Rejmánek and Richardson 1996, Beckman et al. 2011) are two critical mechanisms responsible for the success of non-native plant invasions. To date, experimental manipulations concerning competition and germination have typically been restricted to greenhouse and/or common garden experiments (Thorpe et al. 2011). While this approach has provided enormous insight into ecological theory concerning invasive species, results may not translate easily to the field (Naeem et al. 2000). Currently, the use of field experimental manipulations that incorporate natural variation in the landscape are rare (but see reviews in Stohlgren 2002, Fridley et al. 2007).

Researchers currently recognize that germination success may allow a non-native plant species to become invasive more than competitive ability (Thomson 2005). High germination percentages and early germination are two ways that allow for high germination success (Chrobock et al. 2011). Following germination, species that are capable of successfully colonizing a broader abiotic range are likely to become invasive compared to species with narrow abiotic ranges (Callaway and Josselyn 1992). When considering the colonization of invasive plants, it is important to note that successful colonization following germination may be limited by more than just abiotic soil conditions. Successful establishment following germination is often highest in disturbed habitats with no vegetation (Burke and Grime 1996). For example, germinated seedlings may be prevented from successful colonizing if the surrounding vegetation is capable of preventing enough light penetration to allow germinated seeds to establish. Therefore, when determining the role of germination in the successful colonization of invasive plants it is critical to determine if disturbance is required in order to free up limiting resources and reduce competitive interactions (Davis et al. 2000).

In this study, I explored the roles that germination success and interspecific competition play in the successful invasion of a non-native grass into a native landscape. I conducted a two-year field study in which I compared germination success and competitive interactions across various habitat types commonly found in the prairie landscape. I also conducted an experiment in which I released seeds of invasive smooth brome into disturbed and undisturbed patches of native grass to assess if disturbance was required for seedling establishment in the tall grass prairies. I predicted that invasive plants would have higher germination success and superior competitive ability across various habitats than native species. To test my predictions I used smooth brome (*Bromus inermis* Leyss.), an invasive plant species commonly found across the tallgrass prairies of North America. Currently, there is little information regarding the mechanisms responsible for the successful invasion of smooth brome (but see Otfinowski and Kenkel 2008, Dillemuth et al. 2009, Otfinowski and Kenkel 2008). My research approach is of critical importance when attempting to understand how species are able to invade into non-native communities.

Methods

Invasive Smooth Brome History and Biology

To date, mixed prairie habitat has been reduced by approximately 70% in the Great Plains of North America (Samson et al. 2004). Consequently, prairie habitat has become one of the most imperiled ecosystems in the world (Stoner and Joern 2004). Across the Great Plains of America, smooth brome has heavily invaded prairie habitat. Although, little is known about the invasion process of smooth brome (but see Blankespoor and Larson 1994), despite the fact that its invasive status has been noted (Cronin 2003, Cronin et al. 2004, Cronin 2007, Cronin and Haynes 2004, Haynes and Cronin 2003, Otfinowski et al. 2008, Williams and Crone 2006, Dillemuth et al. 2009). Smooth brome (*B. inermis*), a cool season grass (C_3), was introduced into North America from Hungary and Russia in the late 1880s (Hitchcock 1963) to provide soil retention and animal graze (Larson et al. 2001). Following its introduction, smooth brome has escaped and established in native remnant prairies (D’Antonio and Vitousek 1992). When compared to its close relative, cheatgrass (*Bromus tectorum* L.), a highly noxious weed (USDA and NRCS 2010), smooth brome has been largely ignored as an invasive species, possibly due to its economic value as a forage plant (NISC 2006). To date, there is very little experimental data regarding the factors that contribute to smooth brome's invasiveness, but research has suggested seedling establishment of smooth brome increases with habitat disturbance, elevation of soil nitrogen (Otfinowski and Kenkel 2010) and clonal integration among sibling patches (Otfinowski and Kenkel 2008).

Research Site

I conducted my study at Kelly's Slough National Wildlife Refuge in Grand Forks County, North Dakota. Kelly's Slough was developed to establish and manage wetlands and grasslands unique to the Red River Valley (USFWS 2008). There are four dominant habitat types at Kelly's Slough: (1) Mono-specific stands of the dominant native prairie cordgrass (*Spartina pectinata* Bosc ex Link.) (Hitchcock 1963); (2) mono-specific stands of established invasive smooth brome; (3) mudflats, which are slightly lower in elevation and mostly consist of bare ground and saltwort (*Salicornia rubra* Nels.) in dry periods, and are covered by water in wet periods; and (4) mixed native habitat, which is a mixture of native grasses with no clear dominant species (Cronin and Haynes 2004, Dillemuth et al. 2009). Species in the latter habitat type include foxtail barley (*Hordeum jubatum* L.), western wheatgrass (*Agropyron smithii* Rydb.) and little bluestem (*Andropogon scoparius* Michx.). To determine if competition and germination success vary across the landscape, I conducted my experiments in each of these four dominant habitats.

Germination and Competition Experiment

In order to test if germination success and/or interspecific competition are responsible for the invasion of smooth brome, I sowed seeds of native cordgrass and smooth brome in planting combinations containing the presence/absence of each species within a 1-m^2 plot (Fig. 3.1A). All plots contained four 25 cm x 14 cm subplots evenly spaced within a 1-m^2 area with each subplot

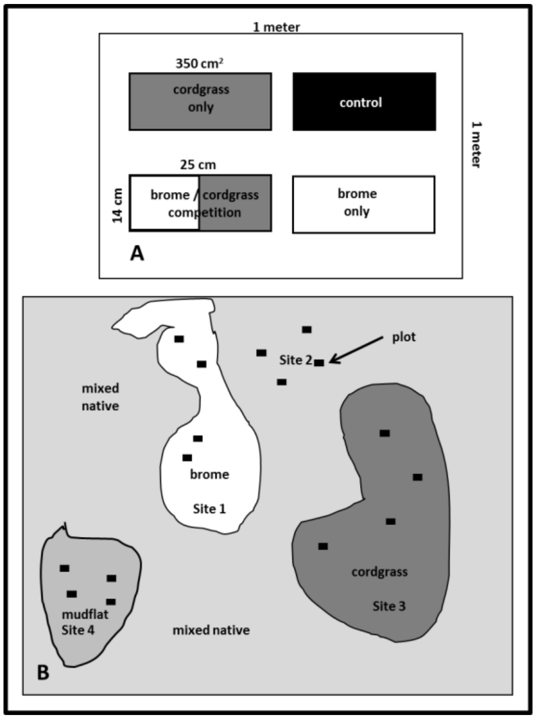


Figure 3.1: Depiction of experimental design. Part A represents subplots within a plot where each plot contains one of all possible planting combinations and part B represents one of the seven replications of sites.

containing one of all possible planting combinations. Overall, this study consisted of 112 plots across seven replicate sites per habitat type (4 plots and 16 subplots within a site) (Fig 3.1B). Following the sowing of seeds into individual subplots, I first measured initial germination in early June 2007, approximately two weeks after I observed the germination of seeds from both species. Then, to test for potential interspecific competitive effects between species, I measured mean number of stems per number of seeds released, mean plant height (cm) and percent of flowering stems (# stems in flower/ total stems) in late July 2007, early June 2008 and late July 2008 for each species present.

In order to prepare sampling plots, I removed all vegetation within a 1-m^2 area at each sampling plot by spraying the herbicide Glyphomax Plus (Dow AgroSciences LLC, Indianapolis, Indiana, USA), a fast acting herbicide that has no discernible residual effects following initial application (Malik et al. 1989) in June 2006. Three weeks later, I clipped and removed all dead vegetation from the plots. Afterward, I anchored commercial grade weed cloth on top of each plot to prevent the re-sprouting of existing plants or germination of seeds present in the soil. Following the initial setup of study plots, I allowed the subplots to remain covered for a 3 month time period to further ensure that any plants that were not eliminated by the use of Glyphomax were prevented from re-sprouting. Leaving subplots covered until winter also prevented the dispersal of new seeds into subplots.

I collected seeds for this experiment from prairie fragments within 1 km of my field site. In late November 2006, I added seeds into each subplot. Seed-addition treatments were assigned at random to the four subplots within each plot. In the single species subplots, I added either 40 ml of smooth brome or cordgrass seed. In the mixed species subplots, I added 20 ml of smooth brome and 20 ml of cordgrass seed. Smooth brome and cordgrass have similar numbers of viable seeds per 40 ml volumes (t_{19}= 1.142, p>0.3) (F. P. Dillemuth, unpublished data). Therefore, the single- and mixed-species subplots had similar total numbers of seeds (40 ml ≈ 200 seeds). Finally, the control subplots had no seeds added in order to allow me to determine if new rhizome growth or seedling dispersal occurred in the subplots.

As part of this study, I wanted to account for the environmental heterogeneity within this experiment in order to assess how abiotic soil conditions may influence the performance of both smooth brome and cordgrass. Therefore, in June 2007 I measured several soil variables (i.e., elevation, salinity, pH, total nitrogen and percent moisture) that may have affected smooth brome and cordgrass performance (Haynes 2004, Williams and Cronin 2004, Dillemuth et al. 2009). I measured soil elevation with a survey grade Leica Geosystems 500 GPS. Following the collection of positional data, I post-processed all data in the program Leica GIS Data Pro to achieve a margin of error of < 1 cm. I collected soil core samples from the upper 20 cm from each plot. Percent soil moisture was determined as the ratio of dry to wet mass (g). Total soil nitrogen from soil samples was assessed through dry combustion by a Leco CN Analyzer (St. Joseph, MI) at Louisiana State University’s Agriculture Research Center for Soil Testing and Plant Analysis Lab. Soil salinity and pH were determined using the standardized procedures developed by the United State Department of Agriculture and Natural Resource Conservation Service Guidelines (USDA-ARS and NRCS 1998). Soil salinity was determined with a benchtop salinity meter after mixing 30 ml of ground soil samples with 30 ml deionized water. After recording salinity, samples were left undisturbed for 15 minutes, after which time a pH benchtop meter was used to determine pH. Every two weeks during the growing season (from May 2007 to August 2008), all non-target species were hand pulled from the subplots. Maintenance of the subplots was conducted every two weeks in order to get non-target species before they establish an extensive root system and therefore I was able to minimize soil disturbance when removing plants. There was also no difference between non-target species among treatment levels indicating an equal maintenance effort across the experiment.

Smooth Brome Germination and Disturbance

To assess whether smooth brome can invade undisturbed cordgrass habitat, I sowed smooth brome seeds into patches of cordgrass in which vegetation was either removed or left undisturbed. Plots used for disturbance treatments were the same cordgrass sites in which I sowed only smooth brome seeds in subplots described in the above paragraph. For the undisturbed treatment, I randomly selected seven prairie cordgrass patches that were not used for the previous experiment. Each undisturbed cordgrass patch represented one site and consisted of four 1-m^2 plots staked out within the patch with two subplots (25 cm x 14 cm) paired in each plot. I then sowed seeds of smooth brome in one subplot in each plot and left the remaining subplot alone to serve as a control. Following germination, I collected data in the same manner as described above. Maintenance was not required for this portion of the study because there were no non-target species in any of the subplots while this portion of the experiment was conducted.

Statistical Analysis

I used Linear Mixed Models to assess the effects of treatment application on the dependent variables. The treatments consisted of habitat type (smooth brome, cordgrass, mixed grasses and mudflat), species planted (smooth brome or cordgrass) into the subplot, and species composition (species alone or in combination with the other species), on each of the following dependent variables: percent germination, number of plant stems per number of seeds released, mean stem height, and proportion of stems in flower. For mean stem number, mean stem height and proportion of flowering stems, I restricted analyses to the final census for two reasons. First, during the first year of this experiment, I had very high stem densities and low plant height when compared to average densities commonly found in un-manipulated areas where both species grow naturally. High stem densities and small plant height were likely a result of the high number of viable seeds sown into subplots to ensure germination success. For example, the average number of plant stems and height of cordgrass ($\bar{x}_{stem}$=17.33 ± 1.8 6 cm, $\bar{x}_{height}$=52.83 ± 2.06 cm) and smooth brome ($\bar{x}_{stem}$=18.44 ± 2.24 cm, $\bar{x}_{height}$=33.67± 1.16 cm) that were naturally occurring in my field site were significantly different from number of stems and plant height of cordgrass ($\bar{x}_{stem}$=25.93 ± 1.96 cm, $\bar{x}_{height}$=15.55±0.48 cm) and smooth brome ($\bar{x}_{stem}$=51.29 ± 3.18 cm, $\bar{x}_{height}$=14.76 ± 0.53 cm) when compared to single species treatments in July 2007 (F. P. Dillemuth, unpublished data). By the time of the final census average stem numbers and plant height for cordgrass ($\bar{x}_{stem}$=18.44 ± 2.11 cm, $\bar{x}_{height}$=51.62 ± 1.57 cm) and smooth brome ($\bar{x}_{stem}$=22.56 ± 2.53 cm, $\bar{x}_{height}$=34.81 ± 1.26 cm) in single species plots were more comparable to naturally occurring stem densities. Secondly, smooth brome is a cool season grass that regenerates new growth and earlier flowering following overwintering dormancy than prairie cordgrass, a warm season grass. Therefore, I realized that any initial differences in plant height and flowering recorded early in the growing season (i.e., initial spring census) might be due to differences in the timing in which each species begins growing. By only using the final census period, I was confident that both species had time to equilibrate towards the natural range of stem densities and plant heights commonly found in well-established patches of both species. Random variables included in the model as covariates were soil conditions (incorporated as a habitat*species planted*abiotic soil measurement interaction) measured and the individual plot containing all possible combinations of the two species. To determine how each dependent variable (percent germination, mean stem height, stem number and flowering) changed with changing levels in soil variables I incorporated each soil variable into the models as a random habitat*species planted*soil variable interaction (Montgomery 2008). By incorporating the habitat*species planted*soil interaction term I was able to estimate the slope and 95% confidence interval for each dependent variable for each species within each habitat. For example, I was able to compare how germination of smooth brome and prairie cordgrass seeds changed independently with changing levels of salinity in each habitat. I would have liked to incorporate the species composition treatment (planted alone or in combination with one another) with the soil interaction term, but doing so did not yield model matrices that converge. Without model matrix convergence, estimates for effects on dependent variables can be unreliable. Plot was included as a random effect to account for the potential spatial autocorrelation at the subplot level (Everitt and Howell 2005, Hegland et al. 2010).

There was evidence for multicollinearity between % moisture and % nitrogen (r = 0.66) in the soil as well as between pH and soil salinity (r = 0.42) requiring I drop one variables from each of the pairs. I excluded % nitrogen from the models because research has shown that soil moisture has the ability to affect uptake of nitrogen (Benning and Seastedt 1995). In addition, percent nitrogen was based on total soil nitrogen and I was unable to determine the relative amount of usable nitrogen available plant growth. By leaving % moisture, I felt that results would provide more insight than trying to interpret total % soil nitrogen. Soil salinity was kept in the analyses because C_4 plants (i.e. *Spartina*) generally have a higher water-use efficiency than C_3 plants (i.e. *Bromus*) in high saline environments (Black 1973) which could give a competitive advantage to prairie cordgrass in areas of high salinity and during periods when soil moisture is low. I removed pH from the analyses because less is known concerning the underlying mechanisms responsible for soil pH impacts on plant performance (Perelman et al. 2001). The distribution of percent germination and the number of plant stems were right skewed, therefore I transformed these data using the natural log method and all soil variables were log transformed as recommended by Palmer (1993) in order to normalize soil variables. I used Residual/Restricted Maximum Likelihood (REML) analysis to produce unbiased estimates of variance and covariance parameters and a Type III test for fixed effects (Systat 2004, Bolker et al. 2009). For all mixed models in this experiment, I incorporated all possible main and interactive fixed effects that were likely to alter the outcome of the dependent variables. I examined all significant fixed effects with a Bonferroni adjusted post-hoc hypothesis test to determine if differences within treatment combinations were significant.

To determine the relative importance of each source of variation to predicting each dependent variable (R^2_M; Nagelkerke 1991, Cronin 2011) I used McFadden's pseudo-R^2. In this calculation $R^2_M = 1- [(LL_{Full} – K)/LL_{Intercept}]$, where LL_{Full} and $LL_{Intercept}$ are the log likelihoods for the full and intercept-only models, respectively. K equals the number of predictors in the model. By incorporating K, I allow for a cost to the goodness-of-fit as the number of variables in the model increases. Values of R^2_M range between 0 and 1 but tend to be lower than traditional R^2

values. Pseudo-R^2 values are not interpreted as an absolute measure of explained variance like traditional R^2 values, but serve as an approximate measure of goodness-of-fit (Long 1997). Consequently, pseudo-R^2 estimates the improvement in the model relative to the intercept only model (i.e., null model) and can be used to estimate the percent contribution of a particular subset of model predictors to the goodness-of-fit (= $\%R^2_M$). Here, $\% R^2_M = R^2_M$ (full) - R^2_M (subset)/ R^2_M (full). The higher $\% R^2_M$ value following the removal of a particular variable indicates a large contribution to the goodness-of-fit to the full model.

Results

Germination Success

During the initial census in May 2007, I observed germination of seeds in plots established in all habitat types except mudflat. In addition, there was no germination in control subplots (no seed added) regardless of habitat type. Consequently, I omitted mudflat habitat type and control treatment levels from all subsequent analyses. Overall, native cordgrass percent germination ($\bar{x}$ =14%) was 43% higher than invasive smooth brome ($\bar{x}$ =8 %) ($F_{1, 620}$=4.24, p<0.04). There were no indications of differences in germination of seeds between species in regards to all other fixed effects and their interactions (Table 3.1). There were significant three-way interactions among habitat type*species*salinity ($t_{620} \approx 4.34$, p<0.001) and habitat type*species*elevation ($t_{620} \approx 3.27$, p<0.005) (Table 3.1). As salinity levels increased in the mixed native habitat type there was a decrease in germination for both smooth brome (slope ± 2se = -0.67 ± .22) and native cordgrass (slope± 2se= -0.44 ± 0.28) (Table 3.1). Similar results were found for invasive smooth brome in cordgrass habitat type (slope ± 2se = -0.38 ± 0.28). Neither species was affected by salinity in the invaded smooth brome habitat type. There was a positive relationship between elevation and percent germination of smooth brome (slope ± 2se = 43.64 ± 21.36) and prairie

Table 3.1: Mixed model results for percent germination of seeds. Type III test for fixed effects indicate if significance was met for fixed factors (e.g. habitat, single/mixed species subplots, species and all interactions) and prediction of random effects indicate significance and slope for abiotic soil (salinity, % moisture and elevation) effects for species within each habitat.

Linear Mixed Model Results for Percent Seed Germination				
Type III Tests for Fixed Effects				
Effect			**F-ratio**	**p-value**
HABITAT			2.185	> 0.11
SPECIES COMPOSITION			0.010	> 0.90
SPECIES			**4.236**	< **0.04**
SPECIES COMPOSITION *SPECIES			1.862	> 0.17
HABITAT*SPECIES COMPOSITION			0.167	> 0.85
HABITAT*SPECIES			2.207	> 0.11
HABITAT*SPECIES COMPOSITION*SPECIES			0.188	> 0.83
Prediction of Random Effects				
Abiotic Factor	**Habitat**	**Species**	**t**	**p-value**
Salinity	**Brome**	**Brome**	-0.319	> 0.75
		Cordgrass	-0.139	> 0.90
	Cordgrass	**Brome**	**-3.408**	< **0.001**
		Cordgrass	-0.476	> 0.63
	Native	**Brome**	**-4.806**	< **0.001**
		Cordgrass	**-3.166**	< **0.002**
Percent Moisture	**Brome**	**Brome**	-0.901	> 0.37
		Cordgrass	-0.146	> 0.88
	Cordgrass	**Brome**	-0.461	> 0.65
		Cordgrass	1.204	> 0.23
	Native	**Brome**	0.371	> 0.71
		Cordgrass	1.496	> 0.14
Elevation	**Brome**	**Brome**	0.401	> 0.69
		Cordgrass	0.610	> 0.54
	Cordgrass	**Brome**	**2.449**	< **0.02**
		Cordgrass	-0.687	> 0.49
	Native	**Brome**	**4.130**	< **0.001**
		Cordgrass	**3.241**	< **0.001**

cordgrass (slope ± 2se = 32.32 ± 19.94) when seeds were sown in mixed native habitat type. Finally, a similar positive relationship was found for smooth brome sown in the cordgrass habitat type (slope ± 2se = 84.95 ± 69.37). R^2_M for the full model was 0.30. The species of seed planted in the subplot contributed the most to the variation in percent germination with contribution to goodness-of-fit of 60% followed by habitat type*species*salinity interaction (22%) and habitat type*species*soil elevation (9%).

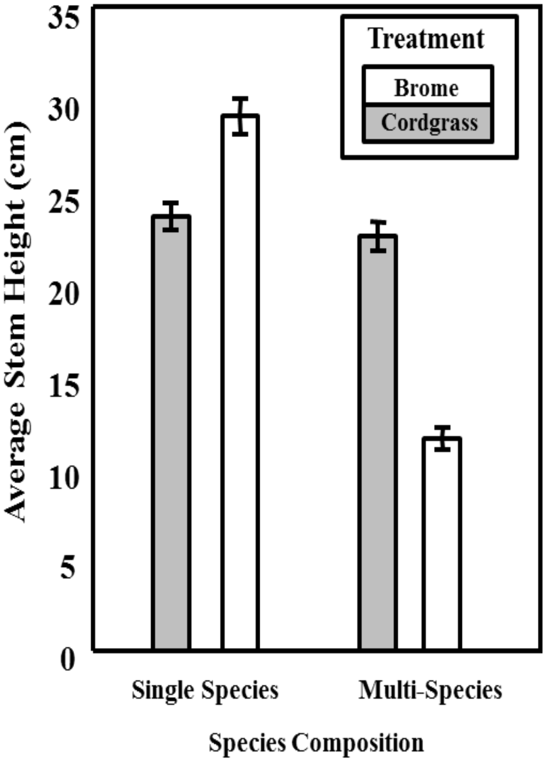


Figure 3.2: The average stem height (cm) ± SE for treatment*species interaction. Single species cordgrass plots were significantly taller than cordgrass competition plots. There was no difference in plant height for brome stems between single species and competition plots. Results presented as sample means and do not reflect actual statistical differences found in using least square means.

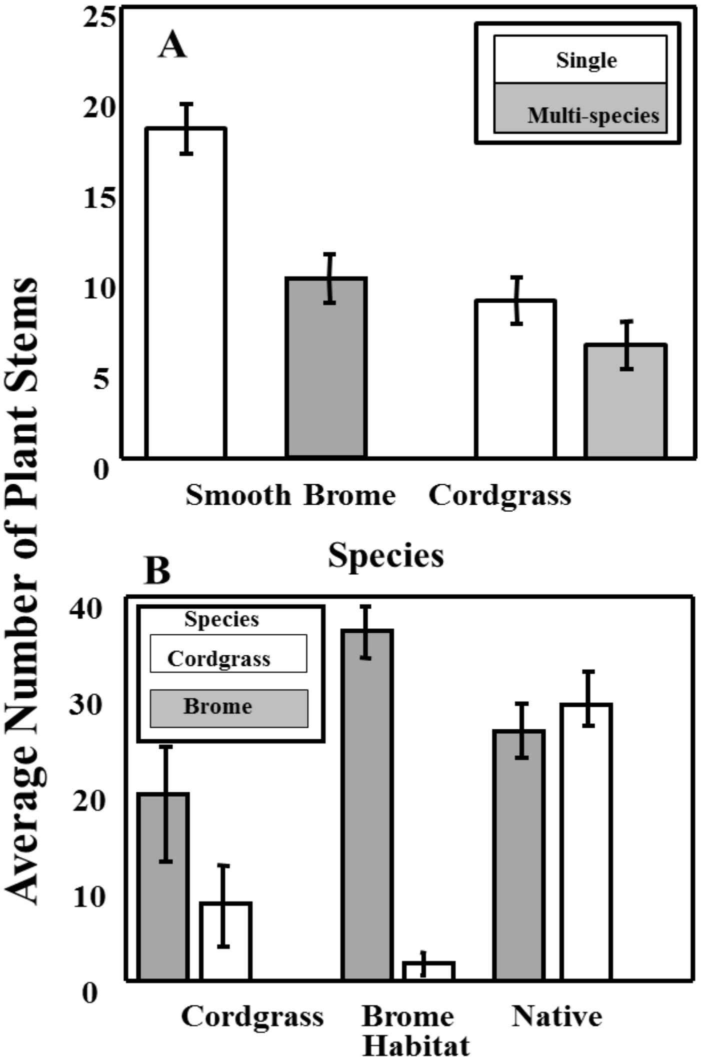
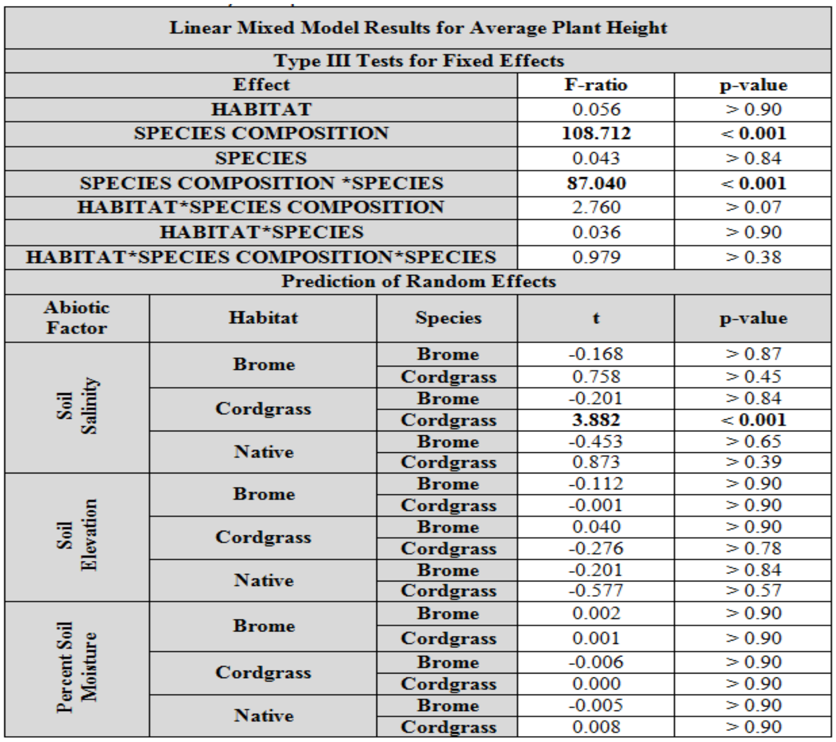


Figure 3.3: The average number of stems ± SE for (A) species composition*species planted interaction and (B) habitat type*species planted interaction. Results presented as sample means and do not reflect actual statistical differences found in using least square means.

When smooth brome seeds were released into undisturbed patches of cordgrass, the percent germination was equal to that of subplots in cordgrass habitat type where vegetation was removed ($F_{1, 120}$= 1.89, p>0.05). Following initial germination, all germinated seedlings of smooth brome in the undisturbed cordgrass patches perished within one growing season. Consequently, I terminated that treatment following the second census period in late July 2007.

Table 3.2: Mixed model results for mean plant height. Type III test for fixed effects indicate if significance was met for fixed factors (e.g. habitat, single/mixed species subplots, species and all interactions) and prediction of random effects indicate significance and slope for abiotic soil (salinity, % moisture and elevation) effects for species within each habitat.



Linear Mixed Model Results for Average Plant Height

Type III Tests for Fixed Effects

Effect	F-ratio	p-value
HABITAT	0.056	> 0.90
SPECIES COMPOSITION	**108.712**	**< 0.001**
SPECIES	0.043	> 0.84
SPECIES COMPOSITION *SPECIES	**87.040**	**< 0.001**
HABITAT*SPECIES COMPOSITION	2.760	> 0.07
HABITAT*SPECIES	0.036	> 0.90
HABITAT*SPECIES COMPOSITION*SPECIES	0.979	> 0.38

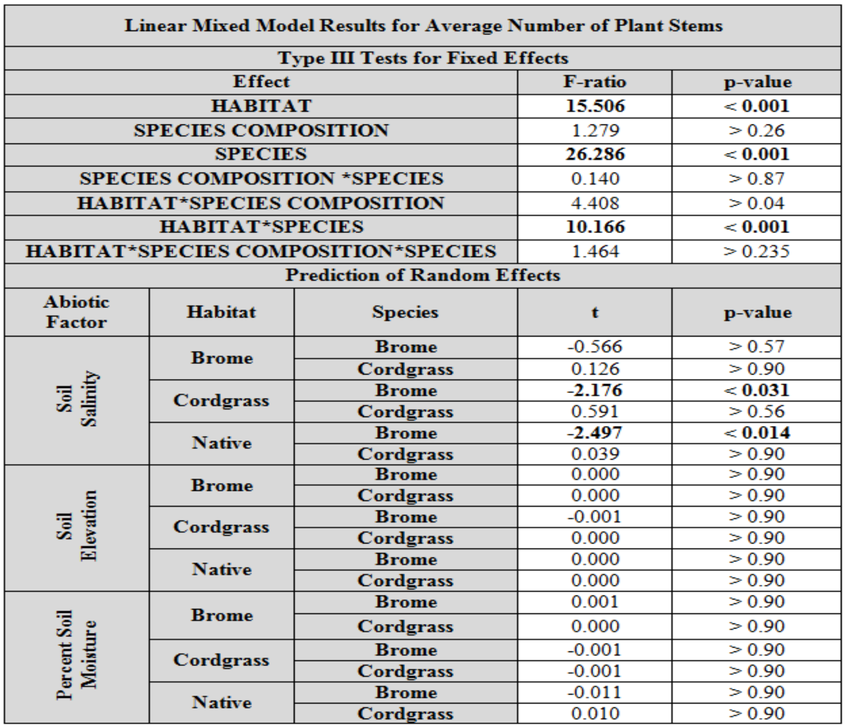
Prediction of Random Effects

Abiotic Factor	Habitat	Species	t	p-value
Soil Salinity	Brome	Brome	-0.168	> 0.87
		Cordgrass	0.758	> 0.45
	Cordgrass	Brome	-0.201	> 0.84
		Cordgrass	**3.882**	**< 0.001**
	Native	Brome	-0.453	> 0.65
		Cordgrass	0.873	> 0.39
Soil Elevation	Brome	Brome	-0.112	> 0.90
		Cordgrass	-0.001	> 0.90
	Cordgrass	Brome	0.040	> 0.90
		Cordgrass	-0.276	> 0.78
	Native	Brome	-0.201	> 0.84
		Cordgrass	-0.577	> 0.57
Percent Soil Moisture	Brome	Brome	0.002	> 0.90
		Cordgrass	0.001	> 0.90
	Cordgrass	Brome	-0.006	> 0.90
		Cordgrass	0.000	> 0.90
	Native	Brome	-0.005	> 0.90
		Cordgrass	0.008	> 0.90

Species Composition and Its Effect on Plant Performance Following Germination

When smooth brome and cordgrass were grown together, native cordgrass plant height was negatively affected when compared to subplots where it was planted alone. When both species were grown together mean cordgrass height ($\bar{x}$ =11.52 cm) was 78% shorter than when cordgrass was grown alone ($\bar{x}$ =51.62 cm) and there was no difference in height of smooth brome when grown alone or with native cordgrass (species composition*species interaction, $F_{1, 83}$=87.04, p<0.001) (Table 3.2, Fig 3.2). Soil salinity had a positive relationship with cordgrass stem height in the cordgrass habitat type (slope ± 2se = 1.24 ± 0.64) (Table 3.2). The stem height model provided a R^2_M value of 0.95 indicating a relatively large improvement from the intercept only model. The variable species composition (grown alone or in combination of one another) contributed the most to the contribution to goodness-of-fit at 92.5% followed by a 5% contribution from both species composition (grown alone or in combination)*species planted (smooth brome or cordgrass) interaction and the habitat type*species*salinity interaction.

Table 3.3: Mixed model results for number of stems per numbers of seeds released. Type III test for fixed effects indicate if significance was met for fixed factors (e.g. habitat, single/mixed species subplots, species and all interactions) and prediction of random effects indicate significance and slope for abiotic soil (salinity, % moisture and elevation) effects for species within each habitat.



Linear Mixed Model Results for Average Number of Plant Stems

Type III Tests for Fixed Effects

Effect	F-ratio	p-value
HABITAT	**15.506**	< **0.001**
SPECIES COMPOSITION	1.279	> 0.26
SPECIES	**26.286**	< **0.001**
SPECIES COMPOSITION *SPECIES	0.140	> 0.87
HABITAT*SPECIES COMPOSITION	4.408	> 0.04
HABITAT*SPECIES	**10.166**	< **0.001**
HABITAT*SPECIES COMPOSITION*SPECIES	1.464	> 0.235

Prediction of Random Effects

Abiotic Factor	Habitat	Species	t	p-value
Soil Salinity	**Brome**	**Brome**	-0.566	> 0.57
		Cordgrass	0.126	> 0.90
	Cordgrass	**Brome**	**-2.176**	< **0.031**
		Cordgrass	0.591	> 0.56
	Native	**Brome**	**-2.497**	< **0.014**
		Cordgrass	0.039	> 0.90
Soil Elevation	**Brome**	**Brome**	0.000	> 0.90
		Cordgrass	0.000	> 0.90
	Cordgrass	**Brome**	-0.001	> 0.90
		Cordgrass	0.000	> 0.90
	Native	**Brome**	0.000	> 0.90
		Cordgrass	0.000	> 0.90
Percent Soil Moisture	**Brome**	**Brome**	0.001	> 0.90
		Cordgrass	0.000	> 0.90
	Cordgrass	**Brome**	-0.001	> 0.90
		Cordgrass	-0.001	> 0.90
	Native	**Brome**	-0.011	> 0.90
		Cordgrass	0.010	> 0.90

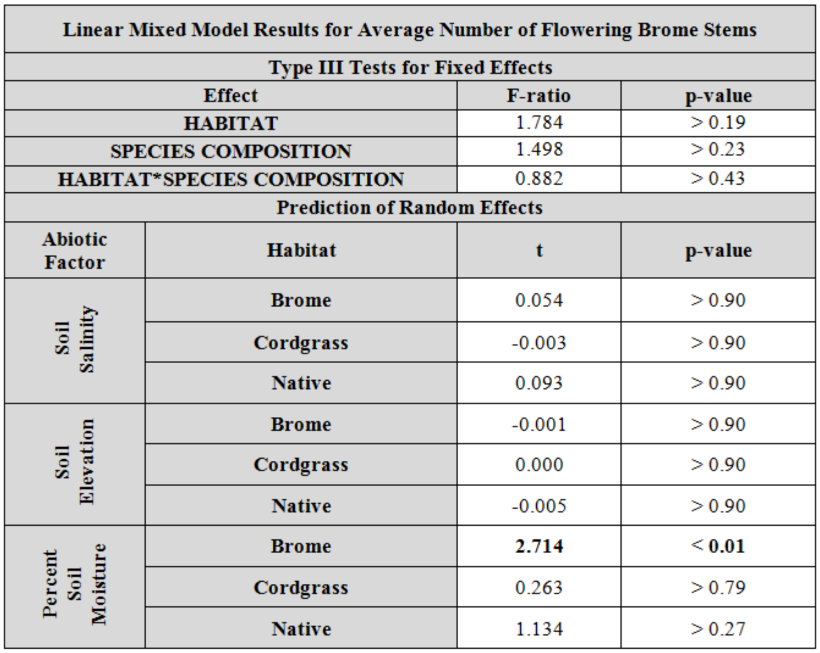
When both smooth brome and cordgrass were grown together, they both had a reduced number of stems when compared to subplots where each species was grown alone. The average number of cordgrass stems when grown with invasive smooth brome ($\bar{x}_{\text{cordgrass}}$=9.78) was 47% lower than the average number of cordgrass stems when grown alone ($\bar{x}_{\text{cordgrass}}$=18.44) (Table 3.3, Fig 3.2A). When smooth brome was grown together with cordgrass ($\bar{x}_{\text{brome}}$=17.69) there was a 35% reduction in average stem number when compared to plots where it was grown alone ($\bar{x}_{\text{brome}}$=27.32). There was also a difference in average stem numbers for each species among habitat type regardless of whether they grew together or alone (Fig. 3.3). Overall, in the invasive smooth brome habitat type the average number of smooth brome stems ($\bar{x}_{\text{brome}}$=34.51) was 94% higher than native cordgrass stems ($\bar{x}_{\text{cordgrass}}$=1.95) and there was no difference in average stem numbers between smooth brome and cordgrass in the cordgrass or mixed native habitat types (Fig 3.2B). Cordgrass in the smooth brome habitat type ($\bar{x}_{\text{cordgrass}}$=1.95) had 94% fewer stems on average when compared to cordgrass stems in the mixed native habitat type ($\bar{x}_{\text{cordgrass}}$=30.82). In the mixed native habitat type, there were more smooth brome stems ($\bar{x}_{\text{brome}}$=21.44) and cordgrass stems ($\bar{x}_{\text{cordgrass}}$=30.82) on average when compared to the cordgrass habitat type ($\bar{x}_{\text{brome}}$ =17.56, $\bar{x}_{\text{cordgrass}}$=17.56). There was a negative effect of soil salinity on stem production for smooth brome in the mixed native habitat type (slope ± 2se = -0.06 ± 0.06) and the prairie cordgrass habitat type (slope ± 2se = -0.06 ± 0.05) (Table 3.3). The stem production model provided a R^2_M value of 0.05 indicating a relatively low improvement from the intercept only model. For stem production, significant fixed variables that contributed the best fit to the model were species planted (smooth brome or cordgrass) (71%), habitat type*species*salinity (22%), species composition* species planted interaction (smooth brome or cordgrass grown alone or together) (15%) and habitat type*species planted interaction (smooth brome and cordgrass plantings across habitat types) (15%).

Finally, I found that smooth brome flowered across all habitat types and there was no flowering of native cordgrass during the duration of the experiment. The only significant factor for smooth brome flowering was a positive relationship with soil moisture (slope ± 2se = 4.48 ± 3.30) (Table 3.4).

Discussion

This study provides further support that interspecific competition (Schmidt et al. 2008, Blank 2010) and germination success (Thomson 2005, Adkins et al. 2011) are important mechanisms responsible for the colonization and establishment of invasive plants. I found that among varying habitats that the invasive species was a better competitor than a dominant native species commonly found in tallgrass prairie systems. Smooth brome had the strongest negative

Table 3.4: Mixed model results for percent flowering stems. Type III test for fixed effects indicate if significance was met for fixed factors (e.g. habitat, single/mixed species subplots, species and all interactions) and prediction of random effects indicate significance and slope for abiotic soil (salinity, % moisture and elevation) effects for species within each habitat.



Linear Mixed Model Results for Average Number of Flowering Brome Stems			
Type III Tests for Fixed Effects			
Effect		**F-ratio**	**p-value**
HABITAT		1.784	> 0.19
SPECIES COMPOSITION		1.498	> 0.23
HABITAT*SPECIES COMPOSITION		0.882	> 0.43
Prediction of Random Effects			
Abiotic Factor	**Habitat**	**t**	**p-value**
Soil Salinity	**Brome**	0.054	> 0.90
	Cordgrass	-0.003	> 0.90
	Native	0.093	> 0.90
Soil Elevation	**Brome**	-0.001	> 0.90
	Cordgrass	0.000	> 0.90
	Native	-0.005	> 0.90
Percent Soil Moisture	**Brome**	**2.714**	< **0.01**
	Cordgrass	0.263	> 0.79
	Native	1.134	> 0.27

competitive effect on the height of native cordgrass followed by a large reduction in stem densities. I observed a 76% and 47% reduction in cordgrass height and stem density, respectively, when grown with invasive smooth brome. In contrast, there was no difference in average plant height of smooth brome and stem density only decreased by 35% in mixed subplots with cordgrass. It is likely that smooth brome affects the height of native cordgrass through competition for light, which is often noted as one of the most important mechanisms responsible for the successful invasion of non-native plant species (Hobbs and Mooney 1986, Hutchinson and Vankat 1997, Mack et al. 2000, Richardson et al. 2000). Smooth brome is a cool season C_3 grass that germinates and resprouts following overwintering dormancy, before prairie cordgrass, a C_4 grass begins to resume growth. Consequently, smooth brome's early growth is likely to limit available light for prairie cordgrass.

I found several abiotic soil interactions among habitats and between species, which indicated that environmental heterogeneity is an important factor concerning invasive and native plant interactions. Soil salinity had a larger effect in the model for stem production than did competitive interactions. These results are in agreement with another study concerning the invasion of ripgut brome (*B. diandrus* Roth.) which is negatively associated with high soil salinity levels (Kolb et al. 2002. Results agree with Kolb et al. (2002) because I found a negative association between germination and stem density of smooth brome as soil salinity levels increased in cordgrass and mixed native habitats. Alternatively, soil salinity levels were negatively associated with germination percentages of cordgrass in the cordgrass habitat type but were positively associated with plant height. The ability of native prairie cordgrass to tolerate higher salinity levels, following establishment, is probably due to its ability to excrete excess salt from its leaves (Marcum 1999) giving it an advantage over invasive smooth brome as salinity levels increase in tallgrass prairies.

For germination success, I predicted that the invasive species would have higher germination percentages compared to a common native species. These findings do not support this prediction as the native species had a higher germination percentage. Even so smooth brome germination was unaffected by habitat or disturbance. The ability to germinate across treatments suggests that smooth brome germination is not limited to specific microhabitats and disturbance regimes. On the other hand, establishment from seed of the invasive species appears to be limited to disturbed areas or areas devoid of cordgrass vegetation. In this experiment, seeds of invasive smooth brome germinated in the core of undisturbed patches of cordgrass but once germinated, these seeds were unable to establish.

Previous research has shown that patches of cordgrass had growth rates that were 2 times greater and extinction rates that were 8 times more likely in areas absent of smooth brome as compared to areas heavily infested with smooth brome (Dillemuth et al. 2009). These findings suggested that invasive smooth brome has the potential to reduce the growth and persistence of native prairie cordgrass. Despite this large effect of smooth brome on cordgrass patch growth and persistence, there was no overall decrease in total cordgrass abundance among field sites (Dillemuth et al. 2009). The lack in overall change in cordgrass coverage indicated that cordgrass was capable of establishing new patches and had high growth rates into areas that were primarily mixed native habitat.

The findings from Dillemuth et al. (2009) suggested that smooth brome may be outcompeting cordgrass, and the experiments in this study were necessary to help verify if competition played a role in invasion success. During the current study, native cordgrass growth was suppressed when grown with invasive smooth brome; however, I did not observe complete displacement of cordgrass by smooth brome. Competitive displacement could occur on a larger time scale than the current study. In Dillemuth et al. (2009) and in this study new patches of smooth brome developing from the center of a cordgrass patch were not observed and all changes in patch size derived from the patch edge. These findings suggest that displacement of cordgrass patches are occurring at the patch edge via interspecific competition of established plants and not through the dispersal of smooth brome seeds into the core of a cordgrass patch. This research support findings from Otfinowski and Kenkel (2008) in which they found that smooth brome ramets remain intact with sibling patches for a period of 2-3 years, providing support for clonal advances into invaded native prairie remnants. Attached ramets can help provide resources to new growth and therefore aid in the displacement of native species.

I observed smooth brome flowering within the first year after seed germination, which may provide an advantage for smooth brome at the early stages of the invasion. Short juvenile stages and early reproductive ability are two characteristics that contribute to the successful invasion of other plant species (Rejmánek and Richardson 1996, Kolar and Lodge 2001).

Management Implications

This manuscript is part of a growing body of literature that focuses on mechanisms responsible for the invasion of smooth brome into tallgrass prairie habitats across North America (but see Wilson 1992, Blankespoor and May 1996, Williams and Crone 2006, Jordan et al. 2008, Otfinowski and Kenkel 2010). Research focusing on smooth brome suggests that leaving prairies idle without actively managing smooth brome will lead to altered local native plant communities (Otfinowski and Kenkel 2008). Active management is necessary because mixed prairie habitat has been reduced by approximately 70% in the Great Plains of North America (Samson et al. 2004) through conversion into farmland. Consequently, prairie habitat has become one of the most imperiled ecosystems in the world (Stoner and Joern 2004).

The use of prescribed fire in prairie ecosystems has been successful in reducing invasive smooth brome populations while increasing the abundance of native species (Wilson and Stubbendieck 2000, Bowles et al. 2003). For example, Wilson and Stubbendieck (2000) found that prescribed fires in early spring, when smooth brome is at the four to five leaf stages, prevents it from consuming limiting resources and flowering. Prescribed fire management allows for the recolonization of warm season grasses, such as prairie cordgrass. Fire is a viable management tool for many land managers if timed correctly. If fires are conducted too early in the growing season, smooth brome is likely to regenerate (Wilson and Stubbendieck 1996) and fires conducted too late in the season are typically not effective at reducing smooth brome abundances (Wilson and Stubbendieck 2000). This study reinforces the importance of prescribed fires before seeds of smooth brome mature and fall to the ground because grassland fires seldom damage seeds on the surface of the ground (Daubenmire 1968). Therefore, if a prescribed fire is conducted after seeds of smooth brome have already set or dispersed and removes standing vegetation, the seeds have a ready-made seedbed increasing the potential to establish in areas where smooth brome was not already present. Late season fires have also shown to be ineffective at reducing smooth brome abundance and therefore if prescribed fires are not conducted at the appropriate growth stage of smooth brome then the fires themselves may help facilitate the invasion. A caution to this approach is that early spring fires can also reduce the abundances of native cool season species (Engle and Bultsma 1984). Therefore, when using fire management as a tool to reduce abundances of smooth brome, it may be critical for managers to monitor the response of native cool season plant species. If fire reduces the abundance of cool season plants then use of reseeding natives may be desirable. Little, if any, research has been done concerning reseeding efforts of cool season grasses following a prescribed fire used for smooth brome reduction. Evaluating the impacts on cool season grasses and reseeding efforts is likely to enhance prairie management efforts.

CHAPTER 4. MULTI-SCALE IMPACT OF AN INVASIVE PLANT ON NATIVE HERBIVORE COMMUNITIES

Introduction

Invasive plants have been considered detrimental to invaded communities and a major cause of ecosystem degradation across the globe (Mack et al. 2000, Carvalheiro et al. 2010) although currently there is little information concerning how invasive plants impact higher trophic levels in invaded communities (Carvalheiro et al. 2010). Once established, invasive plant species can significantly alter native invertebrate species richness (Tallamy and Shropshire 2009, Simao et al. 2010, Almeida-Neto et al. 2011), diversity (Carvalhero et al. 2010, Hartley et al. 2010, Wu et al. 2009) and evenness (Carvalheiro et al. 2010). Changes in invertebrate communities can alter the food web leading to changes in the physical environments (Hladyz et al. 2011, Schirmel et al. 2011), disrupt ecosystem functions leading to alterations in nutrient recycling (Page et al. 2010) and alter predator/prey interactions within invertebrate communities (Gratton and Denno 2006). For example, Schirmel et al. (2011) found that the invasive moss *Campylopus introflexus* led to a reduction of native grass cover and this reduction, in turn, limited food availability for native phytophagous carabid beetles. Subsequently, the reduction of food availability led to a reduction in species richness of the phytophagous carabid beetles in invaded sites compared to sites that were not invaded. Considering that herbivores are necessarily sensitive to changes in plant communities (Southwood et al. 1979, Brown and Southwood 1983, Brown and Hyman 1986, Steffan-Dewenter and Tscharntke 1997) and are likely to be affected during the invasion process, I focused my research on the potential impacts of an invasive grass on the herbivore community in the tallgrass prairies of the Midwestern United States.

Examination of factors affecting herbivore assemblages requires attention to the scale in which research is conducted because results are likely to vary with the scale at which measurements were made (Whittaker 1975, Clarke and Crame 1997, Clarke and Lidgard 2000). Currently little research has examined how spatial scale of measurement influences results describing interactions between plant invasions and native herbivore species (but see Ellingson et al. 2002, Rand et al. 2004). Ellingson et al. (2002) found that a native cicada species abundance was unaffected by invasive saltcedar (*Tamarix* spp.) at a small scale (i.e. few number of trees). However as they increased the spatial scale of their research, they found that large, continuous stands of saltcedar formed a closed canopy creating an unsuitable habitat for the cicada. As a result, the closed canopy led to a reduction in local population sizes. Therefore, incorporating multiple spatial scales may be a critical component for developing a comprehensive understanding of how invasive plants affect native herbivore species. In return, research conducted in this manner may elucidate how patterns in nature change across spatial scales while providing critical insight into theoretical science (Levin 1992). For this study, I propose a multi-scale assessment to determine the relationship between the coverage of invasive smooth brome (*Bromus inermis* Leyss.) and herbivore species richness, diversity and evenness (RDE hereafter) across three spatial scales: plot level (1-m^2) prairie fragment nested within a watershed and watersheds. I looked at RDE because each index can provide insight into how herbivore assemblages change as smooth brome abundance increase across spatial scales. First herbivore species richness (S) gives an indication as to how many species are present. Species richness is limited because it does not account for the relative abundance if each species present therefore species diversity (H) was also measured to give an indication of how many individuals there were relative to the total number of species present. When measuring species richness and diversity it is also easy to calculate an evenness index. Evenness accounts for the observed diversity divided by the maximum possible diversity (H_{max} = H/ lnS) giving a relative indication of how evenly distributed species are within a given brome coverage or spatial scale.

Currently there are no known smooth brome specialist herbivores in North America and therefore herbivores present in brome habitats should be either generalist capable of feeding on smooth brome or herbivore species with the dispersal ability to move through a smooth brome matrix in search of suitable habitat. My prediction at the smallest scale (1-m^2) was that herbivore species RDE are not likely to be strongly affected by high coverage of smooth brome when compared to areas that have little to no smooth brome present. A lack of differences in herbivore RDE is likely because many herbivores have the dispersal ability in which they can readily move through patches at the 1- m^2 spatial scale while searching for a suitable habitat. At larger spatial scales (prairie fragment and watershed), I predicted that as the area covered by smooth brome increased it would likely displace a diverse community of native plants (Otfinowski et al. 2007) that support a diverse suite of specialist and generalist herbivore species adapted to feeding on native plants. A shift in plant communities would then result in an herbivore community dominated by a few generalist herbivores that are capable of feeding on smooth brome. Therefore, at larger spatial scales I predicted that as smooth brome coverage increased there would be a decrease in herbivore species richness and diversity. If predictions for herbivore species richness and diversity are correct at the prairie fragment and watershed scales, I expect that species evenness will increase. This increase in herbivore species evenness would result from a reduction in herbivore species richness as the coverage of smooth brome increases, leading to a community dominated by a few herbivore species capable of feeding on smooth brome.

Methods

Study System

Across the Great Plains of North America, the vast majority of native prairie habitat has been converted to agricultural uses resulting in isolated prairie fragments composed of mainly native vegetation (Stoner and Joern 2004, personal observation). Many species originally introduced for agricultural purposes have subsequently spread into native prairie remnants. One species of particular concern is smooth brome, which is spreading and establishing across tallgrass prairie fragments of the Midwestern United States (D'Antonio et al. 1992; Dillemuth et al. 2009). Smooth brome was originally introduced into North America in the late 1880's from Hungary and Russia (Hitchcock 1963) for soil retention and to provide animal graze (Larson et al. 2001). Currently, research has shown smooth brome has negative effects on a native grass species, prairie cordgrass (*Spartina pectinata* Bosc ex Link.) by suppressing patch growth and increasing patch extinction (Dillemuth et al. 2009). Field experiments have shown that when smooth brome is grown in direct competition with prairie cordgrass that smooth brome reduces prairie cordgrass stem density by 47% and decreases plant height by 76% (See chapter 3).

To date, research indicates that invasive smooth brome has negative effects on a select few native arthropod species (Haynes and Cronin 2003; Baum et al. 2004; Cronin 2003*ab*; Cronin and Haynes 2004; Cronin et al. 2004; Cronin 2007). For example, smooth brome promotes high rates of dispersal of a planthopper (*Prokelisia crocea*) and its parasitoid (*Anagrus columbi*) among patches of prairie cordgrass, and this behavior results in local extinction in isolated prairie cordgrass patches (Cronin and Haynes 2004; Cronin 2007). The effects smooth brome has on *Prokelisia* and *Anagrus* may be just one of many ways smooth brome affects native herbivore species richness, diversity and evenness. The impact of smooth brome on native herbivores could go further than on just a few species and may have large effects on resident herbivores in the tallgrass prairies.

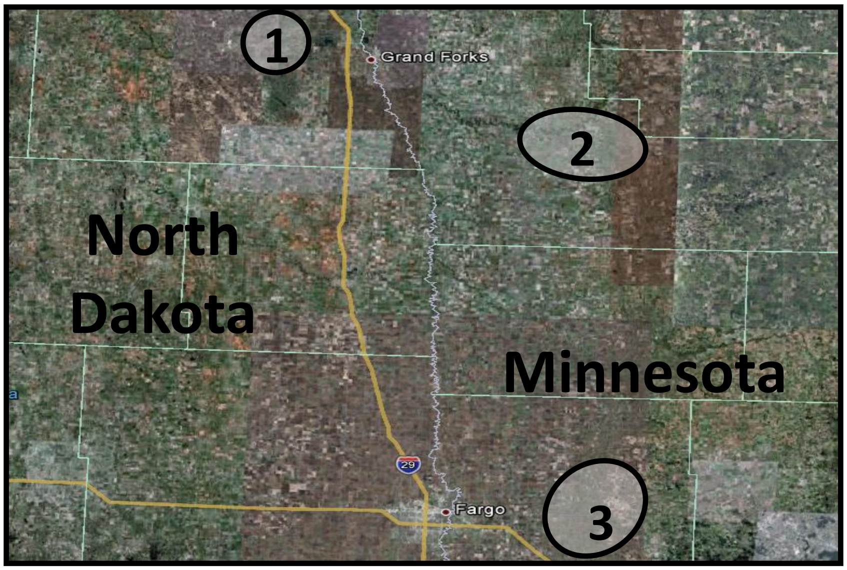


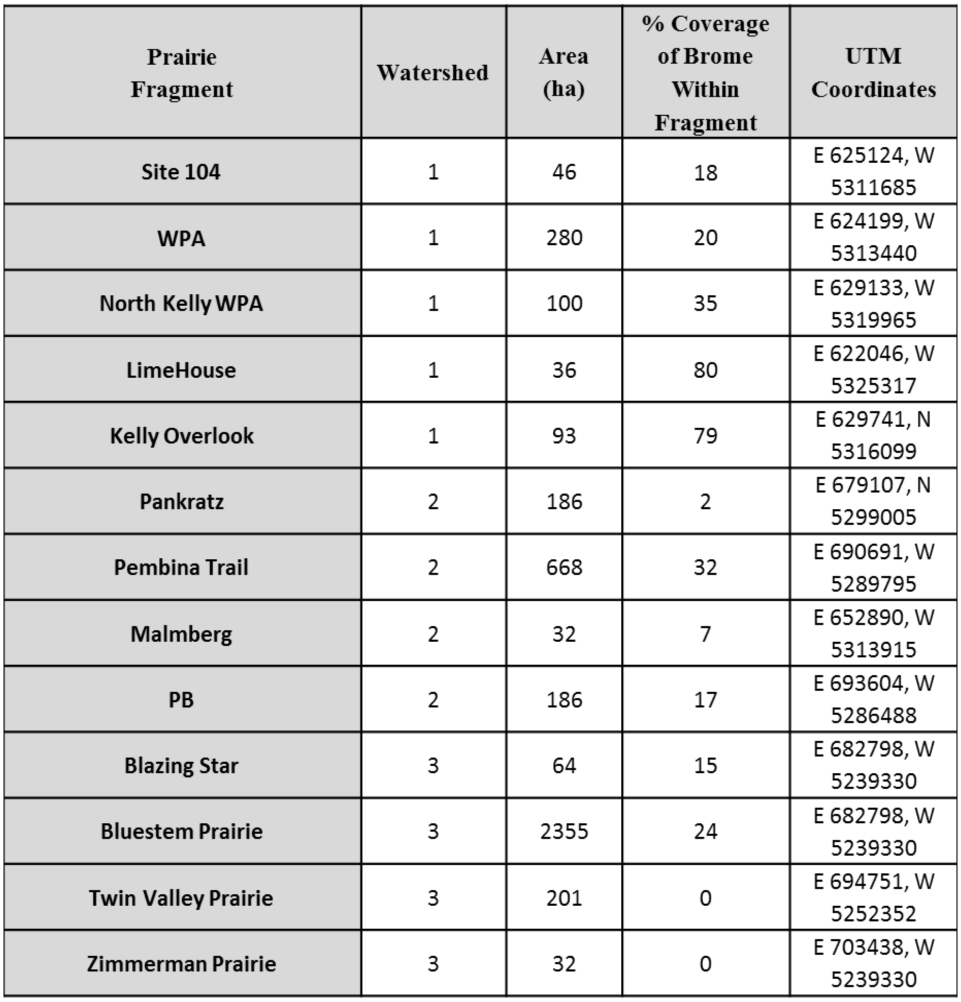
Figure 4.1: Visual representation of the three watersheds used in the survey. For spatial reference, the distance between Grand Forks and Fargo is approximately 130 km.

In eastern North Dakota and western Minnesota, the United States Fish and Wildlife Service (USFWS), The Nature Conservancy (TNC) and the Minnesota Department of Natural Resources currently protect several large watersheds to provide breeding habitat for migratory birds, preserve native biodiversity and protect water quality within agriculturally developed landscapes. These protected areas are composed of discrete and isolated prairie fragments that are embedded within the agriculture landscapes. Prairie fragments are continuous stands of protected native plants that can vary in size (36 -2,355 hectares; this study) (Stoner and Joern 2004, personal observation). I chose three different watersheds for the regional scale, the largest scale to study. I then selected 13 different prairie fragments (among and within prairie fragment scale) that vary in the coverage (0-80%) of invasive smooth brome (Fig 4.1, Table 4.1).

Sampling Design

Within each prairie fragment I selected five 100 m transects which were used to collect herbivore samples. In June 2007 transects were set up so that they were at least 100 meters from

Table 4.1: Description of each prairie fragment drainage, fragment size (ha), percent coverage of smooth brome and spatial location.



Prairie Fragment	Watershed	Area (ha)	% Coverage of Brome Within Fragment	UTM Coordinates
Site 104	1	46	18	E 625124, W 5311685
WPA	1	280	20	E 624199, W 5313440
North Kelly WPA	1	100	35	E 629133, W 5319965
LimeHouse	1	36	80	E 622046, W 5325317
Kelly Overlook	1	93	79	E 629741, N 5316099
Pankratz	2	186	2	E 679107, N 5299005
Pembina Trail	2	668	32	E 690691, W 5289795
Malmberg	2	32	7	E 652890, W 5313915
PB	2	186	17	E 693604, W 5286488
Blazing Star	3	64	15	E 682798, W 5239330
Bluestem Prairie	3	2355	24	E 682798, W 5239330
Twin Valley Prairie	3	201	0	E 694751, W 5252352
Zimmerman Prairie	3	32	0	E 703438, W 5239330

any anthropogenic edges (i.e. roads, trails, culverts, etc.). Each transect consisted of 11 1-m^2 sampling plots that where spaced 10 meters apart. Sampling plots were inspected and the percent coverage of brome was recorded as being in one of the following categories: (1) < 25%, (2) 25–50%, (3) 50–75%, and (4) > 75–100% smooth brome coverage (Dillemuth et al. 2009). I also estimated plant species richness at the plot level because plant richness is known to influence herbivore species richness and abundances (Gerber et al. 2008). At the fragment level, the percent coverage was estimated as the mean coverage among plots within a prairie fragment, and at the watershed scale, the percent coverage was the average among fragments within a watershed.

In order to estimate herbivore species richness, diversity and evenness I used sweep net sampling for a period of one minute at each 1-m^2 plot to collect herbivore samples. This method of sampling is biased towards above ground external feeding herbivores and internal feeders that are searching for a new host plant. However, I felt this method of sampling provided an adequate sample of aboveground herbivores, the focus of this study. Sweep net sampling has also been shown to provide a good measure of relative species richness and abundance in grassland systems (Evans et al. 1983). All collected material was placed in a Ziploc bag and stored on ice. Following a day's collection, all samples were frozen until identified and counted. I collected sweep samples in early June and late July of 2007 and 2008. These collection periods corresponded with peak abundances of arthropod communities in this system (personal observation). All samples collected in early summer of 2008 were sorted and identified while all other collection periods were sub-sampled due to time constraints of the investigators. Five samples per transect were randomly selected for processing.

Herbivore Identification

Herbivores were first identified to the family level and as new morphospecies appeared, I assigned them a reference number in order to discern them from other morphospecies. This method of sampling has been shown to provide an effective characterization of arthropod communities (Oliver and Beattie 1996). Following identification of all morphospecies, I then researched each family to determine which morphospecies had an herbivorous diet during any part of their life cycle that was capable of causing damage to plant tissue. All morphospecies that were clearly capable of causing plant damage were included in the analyses. Predators and other species that could not be clearly identified as potential herbivores were removed from the data set. I was not able to identify approximately 14 % of individuals as either predators or herbivores. Individuals removed were equally distributed among brome categories and represent a small portion of the total number of individuals collected; their removal from the analyses was not likely to bias results.

To measure the potential changes within the herbivore community as the coverage of smooth brome increased, I used the Shannon-Wiener diversity and evenness indices (Shannon and Weaver 1949) and species richness as the dependent variables in my models. To calculate species richness I pooled data across all four-time periods to get an estimate at the watershed, prairie fragment and plot levels. Species richness was plotted against sample based rarefaction curves in EstimateS using the plot, prairie fragment and watershed spatial scales to ensure that I adequately sampled enough of the community to make inferences concerning species richness at the three spatial scales (Colwell 2009). Chao 1 ± 95% CI was used as the best estimator for richness (Chao 1984; Colwell and Coddington 1994). For my measures of diversity and evenness, I restricted the data analysis to the final collection date in which I had the highest number of replicates and equal sample sizes across fragments. My concern in using data from all collection dates in the analysis was that differences detected might derive from unequal sampling more than actual differences in diversity and evenness. Increased sampling will inherently lead to increased abundances, which are accounted for in these indices. I first calculated the Shannon-Wiener diversity index for each sample collected at the plot level. For prairie fragments and watersheds, I combined total number of individuals for each species present in order to scale up the data to represent the diversity and evenness at each spatial scale.

Statistical Analyses

To determine if smooth brome alters the community assemblages of herbivores I used General Linear Models (GLM) to estimate differences in the dependent variables (herbivore species richness, diversity and evenness) at the plot, prairie fragment and watershed spatial scales. For the plot-level analysis, I accounted for the hierarchical structure of tallgrass prairies by including the following sources of variation in the model: transects nested within prairie fragments, prairie fragments nested within watersheds, and watersheds. Percent smooth brome and plant species richness were also included in the model as fixed effects for the plot level analyses. I omitted transect level analyses because it was an artifact of my design to collect herbivore samples and not a spatial scale of interest. At the spatial scale of the prairie fragment, the only nested factor was prairie fragment within a watershed. At the watershed level, I was also able to incorporate prairie fragment size in the analyses to test for any effects of fragment size on herbivore RDE. For each spatial scale, separate tests were performed for each of the three dependent variables. I compared herbivore RDE for each spatial with a Bonferroni adjustment for the multiple tests due to the non-independence between the models.

Results

Over the course of the 2007 and 2008 growing seasons, I identified 258 herbivorous morphospecies across 36 families and 7 orders (Table 4.2). Overall, herbivore species richness ($\bar{x}_{\text{plot}} = 3.93$, $\bar{x}_{\text{fragment}} = 60.62$ and $\bar{x}_{\text{watershed}} =151$) and diversity ($\bar{x}_{\text{plot}} = 1.11$, $\bar{x}_{\text{fragment}} = 3.19$ and $\bar{x}_{\text{watershed}} = 3.93$) (Table 4.3) increased from the plot level, prairie fragment and watershed, respectively. For species evenness there was a slight decrease in average values for the plot level ($\bar{x}$ =0.89), prairie fragment ($\bar{x}$ = 0.86) and watershed ($\bar{x}$ =0.82) scales, respectively (Table 4.3). Overall there was a relatively good fit for the models of species richness (r^2=0.54, r^2=0.87 and r^2=37), diversity (r^2=0.74, r^2=0.62 and r^2=0.64) and evenness (r^2=0.42, r^2=0.64 and 0.83) at the plot, prairie fragment and watershed levels, respectively.

Table 4.2: Taxonomic breakdown of identified herbivorous morphospecies across all prairie fragments.

Order	Family	Number of Species	Order	Family	Number of Species
Orthoptera	Tetrigidae	1	Thysanoptera	Thripidae	1
	Acrididae	30	Coleoptera	Curculionidae	11
	Romaleidae	1		Tenebrionidae	1
	Tettigoniidae	9		Cerambycidae	2
Hemiptera	Tingidae	1		Chrysomelidae	24
	Acanthosomatidae	1	Hymenoptera	Cephidae	2
	Thyreocoridae	1		Siricidae	6
	Pentatomidae	9		Perilampidae	1
	Lygaeidae	20		Cimbicidae	1
	Blissidae	4		Tenthredinidae	2
	Cercopidae	28		Cynipidae	2
	Membracidae	2		Gasteruptiidae	1
	Cicadellidae	59	Lepidoptera	Pyralidae	1
	Delphacidae	6		Lasiocampidae	2
	Dictyopharidae	2	Diptera	Tephritidae	2
	Acanaloniidae	1		Culicidae	15
	Aleyrodidae	1		Bibionidae	3
	Aphididae	4			
Number of Orders = 7					
Number of Families = 36					
Total Herbivore Morphospecies Richness = 258					

Across the field study, I found several significant variables that affected herbivore species richness at the plot level (Table 4.3). Although, smooth brome did not have a significant relationship with richness ($F_{3, 489}$=0.66), evenness ($F_{3, 125}$=0.24) and diversity ($F_{3, 118}$ =0.36) with all p-values > 0.90 following a Bonferroni adjustment for multiple tests (Fig. 4.2). Plant species richness had a positive relationship with herbivore diversity ($F_{1, 125}$=4.34, p<0.001) and evenness ($F_{1, 125}$=9.06, p<0.01) (Fig. 4.3). Watersheds differed in species richness at the plot level ($F_{2, 489}$=5.55, p<0.01), diversity ($F_{2, 125}$=15.14, p<0.001) and evenness ($F_{2, 118}$=6.89, p<0.003) (Table

4.4). Finally, prairie fragments nested within watersheds were also significant for species richness ($F_{10,\ 125}$=3.04, $p < 0.001$) and diversity ($F_{10,\ 125}$=6.88, $p< 0.006$).

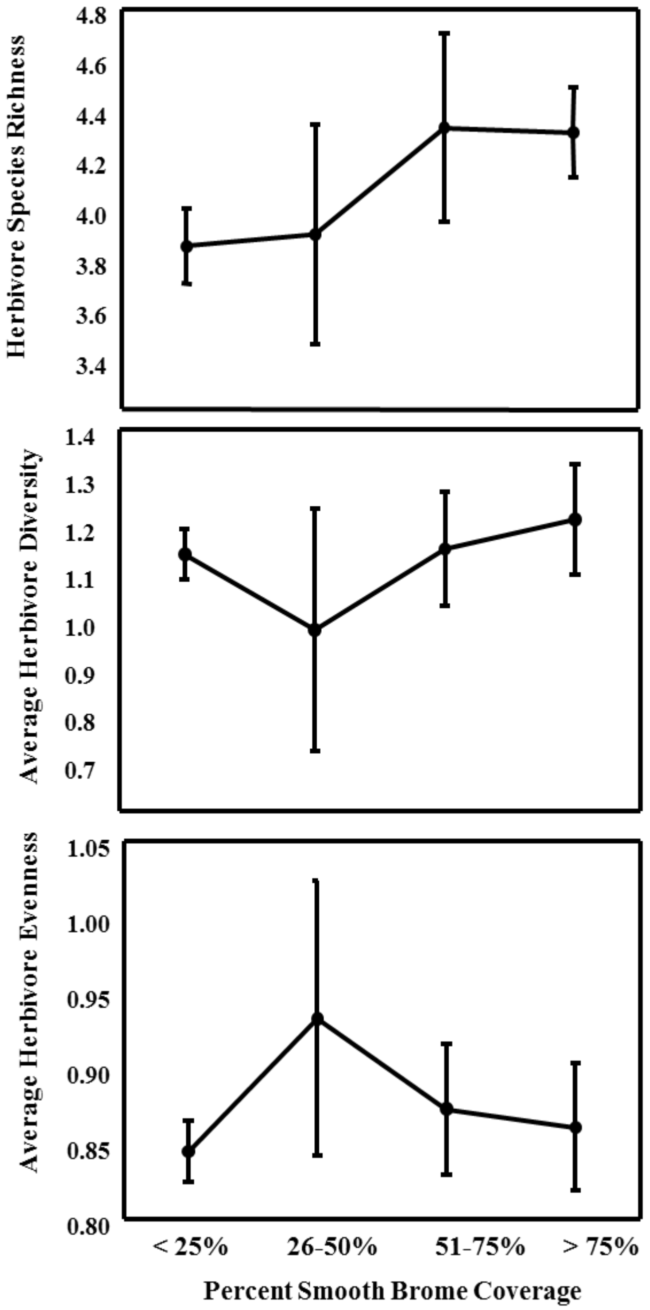


Figure 4.2: Relationship between smooth brome coverage and herbivore species richness, diversity and evenness (mean ± SE) at the plot level.

At the prairie fragments level, I observed a trend that suggested that as the coverage of smooth brome increases there is a decrease in herbivore species diversity and evenness (Fig. 4.4, Table 4.5 and 4.6). For example, when comparing areas with < 25% brome coverage (low coverage: $\bar{x}_{diversity}$=1.97, $\bar{x}_{evenness}$=0.85) with areas that have > 75% coverage (high coverage: $\bar{x}_{diversity}$=1.42, $\bar{x}_{evenness}$=0.64) at the prairie fragment spatial scale I observed a 28% and 24.7% decrease in mean herbivore species diversity and evenness, respectively (Table 4.5). Although the relationship between smooth brome coverage and herbivore species richness ($F_{3,\ 49}$ =1.77, $p > 0.50$), diversity ($F_{3,}$

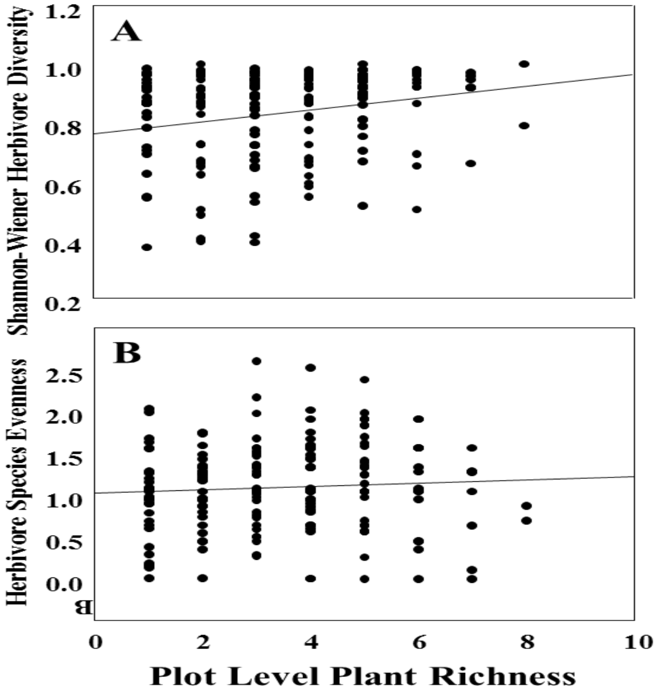


Figure 4.3: Plot level results depicting the relationship between plant richness and (a) herbivore diversity and (b) herbivore evenness.

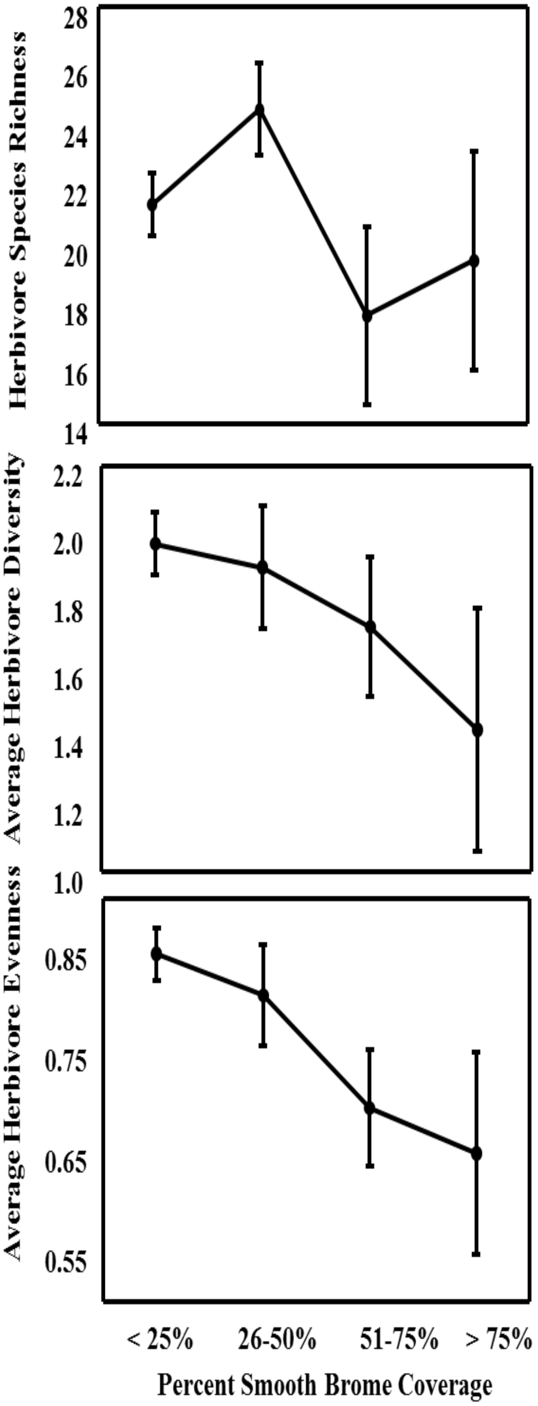
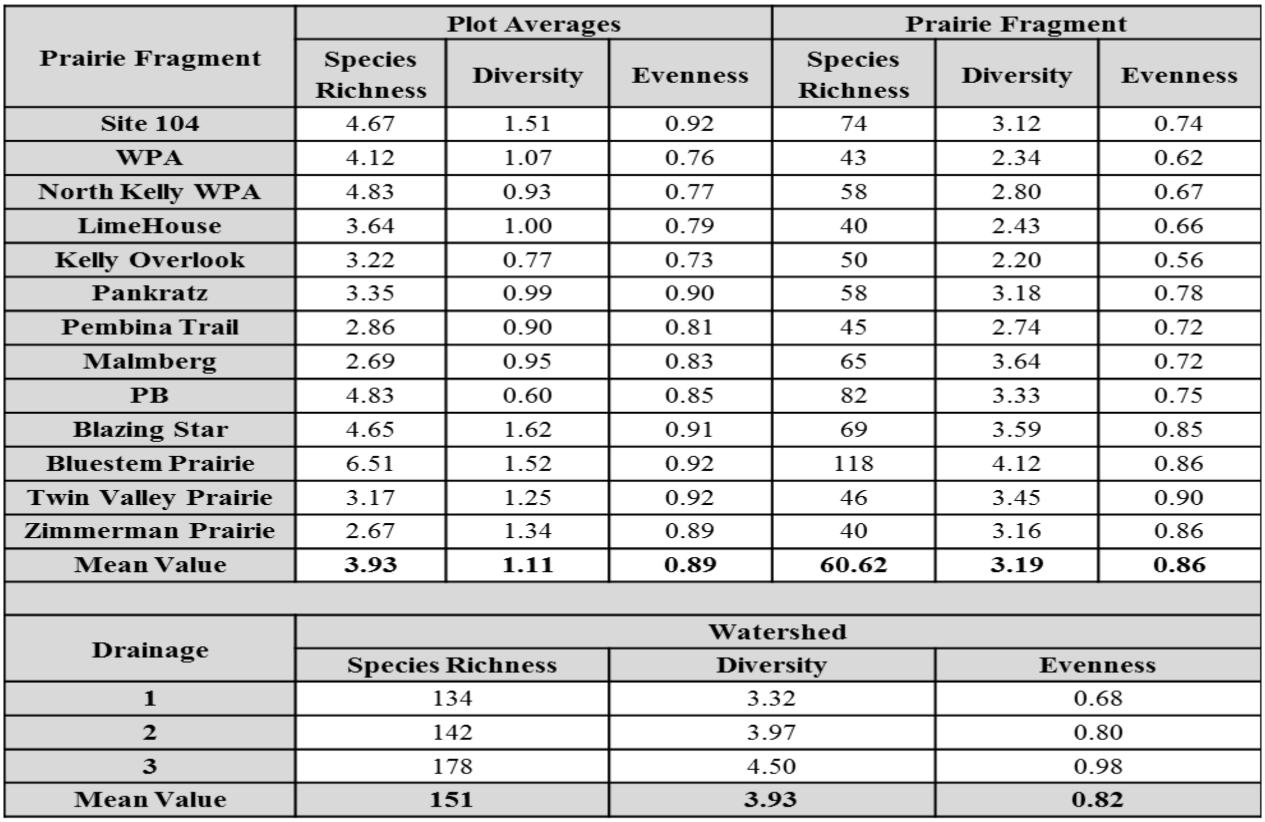


Figure 4.4: Relationship between smooth brome coverage and species richness, diversity and evenness (mean ± SE) for prairie fragment level.

$_{46}$=0.70, $p > 0.90$) and evenness ($F_{3, 46}$= 1.98, $p > 0.39$) were not statistically significant (Fig. 4.4, Table 4.6). The only significant effect at the prairie fragment level was of prairie fragment nested within watersheds ($F_{10, 49}$ =11.93, $p < 0.001$) (Table 4.6).

For watersheds, there was a trend in a decrease in species richness as the coverage of smooth brome increased. I observed a 29% decrease in species richness in areas with >75% smooth brome coverage ($\bar{x}_{\text{species richness}}$ = 68) when

Table 4.3: Average herbivore species richness, diversity and evenness values for each prairie fragment and spatial scale in my study.



Prairie Fragment	Plot Averages			Prairie Fragment		
	Species Richness	Diversity	Evenness	Species Richness	Diversity	Evenness
Site 104	4.67	1.51	0.92	74	3.12	0.74
WPA	4.12	1.07	0.76	43	2.34	0.62
North Kelly WPA	4.83	0.93	0.77	58	2.80	0.67
LimeHouse	3.64	1.00	0.79	40	2.43	0.66
Kelly Overlook	3.22	0.77	0.73	50	2.20	0.56
Pankratz	3.35	0.99	0.90	58	3.18	0.78
Pembina Trail	2.86	0.90	0.81	45	2.74	0.72
Malmberg	2.69	0.95	0.83	65	3.64	0.72
PB	4.83	0.60	0.85	82	3.33	0.75
Blazing Star	4.65	1.62	0.91	69	3.59	0.85
Bluestem Prairie	6.51	1.52	0.92	118	4.12	0.86
Twin Valley Prairie	3.17	1.25	0.92	46	3.45	0.90
Zimmerman Prairie	2.67	1.34	0.89	40	3.16	0.86
Mean Value	**3.93**	**1.11**	**0.89**	**60.62**	**3.19**	**0.86**

Drainage	Watershed		
	Species Richness	Diversity	Evenness
1	134	3.32	0.68
2	142	3.97	0.80
3	178	4.50	0.98
Mean Value	**151**	**3.93**	**0.82**

compared to areas with < 25% smooth brome coverage ($\bar{x}_{\text{species richness}} = 48.33$) (Fig.4.5, Table 4.5 and 4.7). Although there was no significant relationship between the percent coverage of smooth brome and species richness ($F_{3,7} = 0.35$, $p > 0.9$), diversity ($F_{3,7} = 11.93$, $p < 0.001$) and evenness ($F_{2,7} = 2.89$, $p > 0.36$). There was also no significant relationship between the size of a prairie fragment on herbivore species richness ($F_{1,6} = 0.16$, $p > 0.9$), diversity ($F_{1,6} = 0.48$, $p > 0.9$) and evenness ($F_{1,6} = 3.99$, $p > 0.28$).

Discussion

Previous research has shown that invasive smooth brome can lead to local extinctions of a native specialist herbivore (Cronin and Haynes 2004; Cronin 2007), is capable of displacing native plant species (Williams and Crone 2006, Otfinowski et al. 2007, Dillemuth et al. 2009) and is spreading across the tallgrass prairies (D'Antonio et al. 1992). I predicted that I should

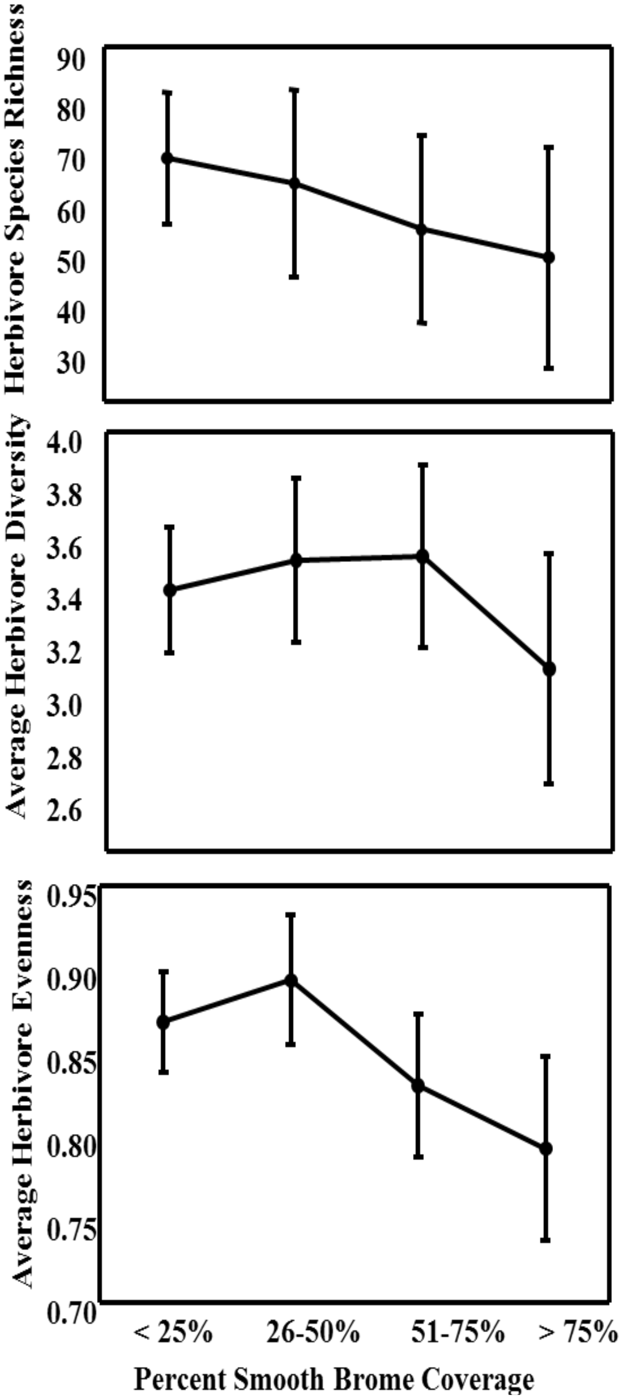


Figure 4.5: Relationship between smooth brome coverage and herbivore species richness, diversity and evenness (mean ± SE) for the watershed level.

find effects of smooth brome on resident herbivores in the tallgrass prairie fragments. Although research has suggested that invasive plants are capable of altering native invertebrate species richness (Tallamy and Shropshire 2009, Simao et al. 2010, Almeida-Neto et al. 2011), diversity (Carvalhero et al. 2010, Hartley et al. 2010, Wu et al. 2009) and evenness (Carvalheiro et al. 2010) I did not find any statistical effect with the spread of smooth brome on RDE. The current study is not the first to detect no changes in RDE in heavily invaded habitats when compared to non-invaded habitats. Hartley et al. (2010) found that in the invasion of Chinese tallow (*Triadica sebifera* L.) harbored similar species richness and abundances of other native tree species, but the community composition of arthropod species differed significantly from the native trees. For species evenness, Schooler et al. (2009) were able to demonstrate that although an increase in invasive

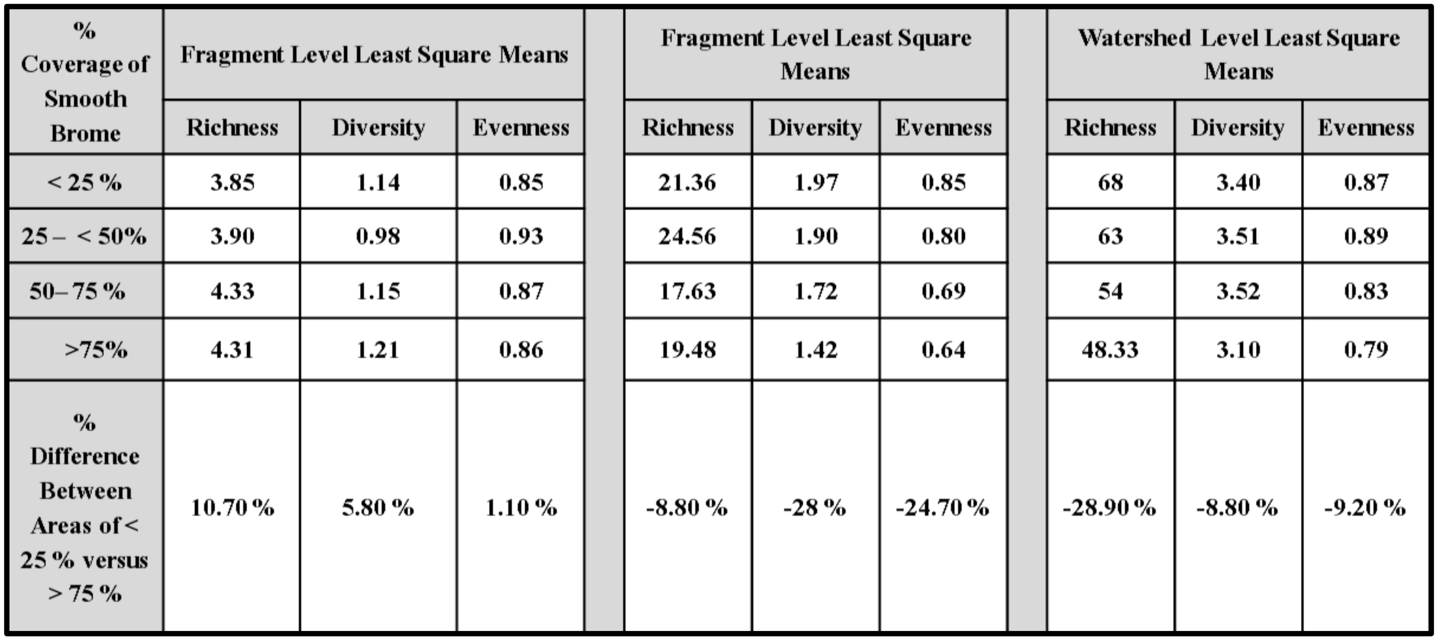
Table 4.4: Representation of plot level results of GLM models for our dependent variables herbivore species richness, diversity and evenness. Variables incorporated in to our model at this scale were percent coverage of smooth brome, plant species richness, watershed, prairie fragment nested within watershed and transect nested within prairie fragment.

General Linear Model Results for Prairie Fragment Level					
Herbivore Species Richness					
Source	**Type III SS**	**df**	**Mean Squares**	**F-ratio**	**p-value**
% Brome	160.02	3	53.34	1.77	>0.50
Watershed	200.79	2	100.39	3.33	>0.13
Fragment(Watershed)	**3,602.31**	**10**	**360.23**	**11.93**	**<0.001**
Error	1,479.19	49	30.19		
Herbivore Species Diversity					
% Brome	0.51	3	0.17	0.70	>0.90
Watershed	0.86	2	0.43	1.78	>0.54
Fragment(Watershed)	3.35	10	0.34	1.39	>0.65
Error	11.13	46	0.24		
Herbivore Species Evenness					
% Brome	0.112	3	0.037	1.983	>0.39
Watershed	0.045	2	0.022	1.190	>0.90
Fragment(Watershed)	0.264	10	0.026	1.399	>0.63
Error	0.867	46	0.019		

plant coverage reduced herbivore abundances the reduction in abundance was uniform among species leading to a non-significant effect on herbivore species evenness. Schooler et al. (2009) also attributed their inability to show an effect of increasing invasive plant coverage on native herbivore species diversity to the same uniform decrease in abundances but not in species richness. Therefore, it is possible that although RDE does not differ with brome coverage that the composition of herbivore assemblages may differ significantly.

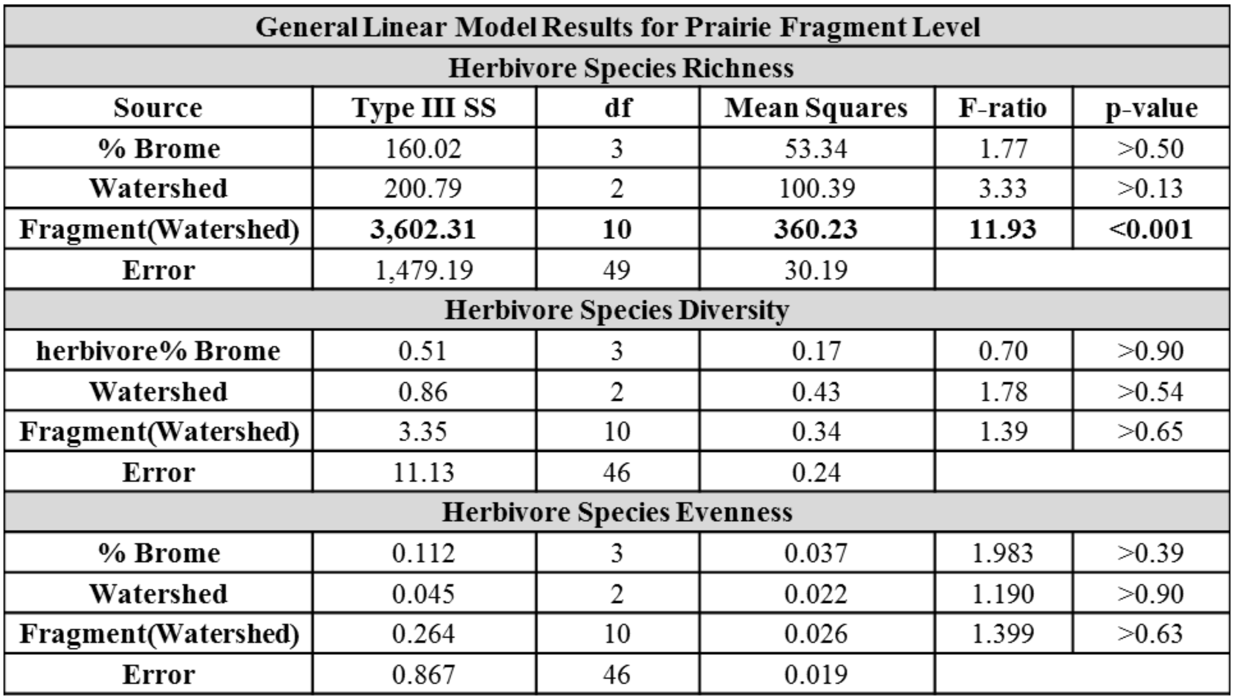
Even though I did not observe any statistically significant effects of smooth brome coverage on RDE, I observed a trend towards a decrease in herbivore diversity and evenness (prairie fragment level) and species richness (watershed spatial scale) as the coverage of smooth brome increased. The observed trends are consistent with other studies that have found that some invasive plants are susceptible to generalist herbivores which leads to a decline in herbivore community richness and abundance as the coverage of invasive plants increases (Litt and Steidl

Table 4.5: Result indicating average herbivore species richness, diversity and evenness for percent coverage of smooth brome at each spatial scale observed.



% Coverage of Smooth Brome	Fragment Level Least Square Means			Fragment Level Least Square Means			Watershed Level Least Square Means		
	Richness	Diversity	Evenness	Richness	Diversity	Evenness	Richness	Diversity	Evenness
< 25 %	3.85	1.14	0.85	21.36	1.97	0.85	68	3.40	0.87
25 – < 50%	3.90	0.98	0.93	24.56	1.90	0.80	63	3.51	0.89
50– 75 %	4.33	1.15	0.87	17.63	1.72	0.69	54	3.52	0.83
>75%	4.31	1.21	0.86	19.48	1.42	0.64	48.33	3.10	0.79
% Difference Between Areas of < 25 % versus > 75 %	10.70 %	5.80 %	1.10 %	-8.80 %	-28 %	-24.70 %	-28.90 %	-8.80 %	-9.20 %

Table 4.6: Representation of prairie fragment of GLM models for my dependent variables herbivores species richness, diversity and evenness. Variables incorporated into my model at this scale were percent coverage of smooth brome, watershed and prairie fragment nested within watershed.



General Linear Model Results for Prairie Fragment Level					
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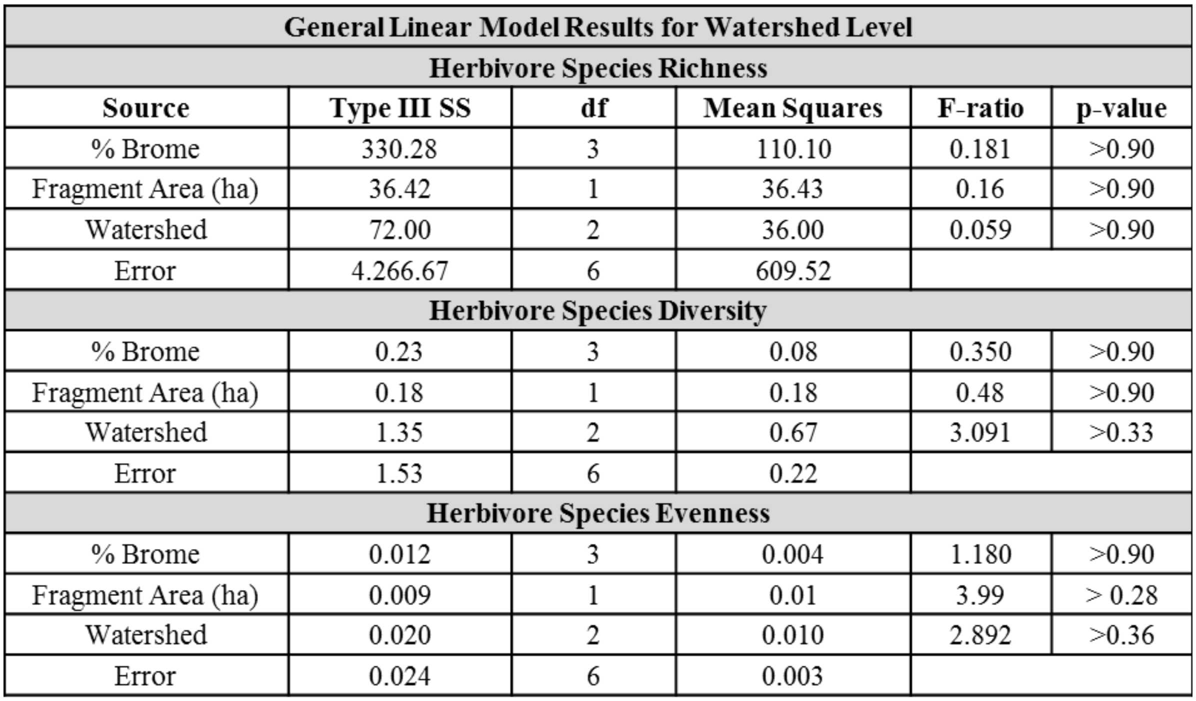
Watershed	0.86	2	0.43	1.78	>0.54
Fragment(Watershed)	3.35	10	0.34	1.39	>0.65
Error	11.13	46	0.24		
Herbivore Species Evenness					
% Brome	0.112	3	0.037	1.983	>0.39
Watershed	0.045	2	0.022	1.190	>0.90
Fragment(Watershed)	0.264	10	0.026	1.399	>0.63
Error	0.867	46	0.019		

2010; Yoshioka et al. 2010). For example, Gerber et al. (2008) observed a decrease in morphospecies richness and biomass of invertebrates across prairie fragments that were infested with invasive knotweeds verses prairie fragments that did not have knotweeds present. Decreases in morphospecies richness and abundances are often attributed to a decrease in native plant richness, which results in a decrease in monophagous and oligophagous herbivores as the coverage of invasive species increases (Valtonen et al. 2006; de Groot et al. 2007). Considering previous research has shown that the invasion of smooth brome can reduce the diversity of native plants (Otfinowski et al. 2007) and smooth brome has no known specialist associated with it, I would expect to see the observed trend in decreasing richness, diversity and possibly evenness as the coverage of smooth brome increased.

At the plot level, I found that an increase in plant species richness resulted in higher herbivore diversity and evenness of herbivore species, but I found no effect on herbivore species richness. The significant effect of plant species richness is likely attributed to an increase of the relative abundance between herbivore species as plant species richness increased resulting in higher diversity and evenness at the plot level. A negative relationship was unexpected because previous research has shown that plant richness is likely to result in an increase in herbivore species richness and a decrease in diversity due to an increase in predator abundance (Haddad et al. 2009). The increase in predator abundance therefore leads to an increase in herbivore abundance in plots with low plant species richness which is opposite of the patterns I found. I observed an increase in herbivore species abundance as plant species richness increased, but there was no change in herbivore species richness. Therefore, the results may have been driven by the reduction in the relative abundance of common species and not among species that were rare in abundance. Currently, there is no clear explanation as to why my observational results differ from the experimental manipulations of Haddad et al. (2009). It is possible that predator communities in my observational study are not comparable to that of Haddad et al. (2009) and incorporating predator species into future observational studies may help explain differences found between observational and experimental approaches.

At the prairie fragment spatial scale, the only significant effect was a prairie fragment nested within watersheds effect on herbivore species richness. Indicating differences in species richness among prairie fragments that were not accounted for in the model. The difference among sites could be driven by plant richness (Fred and Brommer 2003, Schultz and Crone 2005), landscape connectivity (Tack et al. 2010), composition of surrounding matrix and fragment isolation (Hatfield and LeBuhn 2007). For example, Hatfield and LeBuhn (2007) found

Table 4.7: Representation of watershed level results of GLM models for my dependent variables herbivores species richness, diversity and evenness. Variables incorporated into my model at this scale were percent coverage of smooth brome, prairie fragment size and watershed.



General Linear Model Results for Watershed Level					
Herbivore Species Richness					
Source	**Type III SS**	**df**	**Mean Squares**	**F-ratio**	**p-value**
% Brome	330.28	3	110.10	0.181	>0.90
Fragment Area (ha)	36.42	1	36.43	0.16	>0.90
Watershed	72.00	2	36.00	0.059	>0.90
Error	4.266.67	6	609.52		
Herbivore Species Diversity					
% Brome	0.23	3	0.08	0.350	>0.90
Fragment Area (ha)	0.18	1	0.18	0.48	>0.90
Watershed	1.35	2	0.67	3.091	>0.33
Error	1.53	6	0.22		
Herbivore Species Evenness					
% Brome	0.012	3	0.004	1.180	>0.90
Fragment Area (ha)	0.009	1	0.01	3.99	> 0.28
Watershed	0.020	2	0.010	2.892	>0.36
Error	0.024	6	0.003		

that quality of habitat and connectivity among habitats was a more consistent variable than variables they measured within a habitat (i.e. fragment size, grazing regime and habitat moisture levels) when explaining diversity and abundances of herbivore species. Plant species richness and diversity are also known to have larger impacts on native herbivore communities than size of habitat (Hendrix et al. 2010). Unfortunately, I do not have a measure of plant richness within a prairie fragment and therefore I am unable to determine if any relationship exists between plant richness and herbivore RDE at larger spatial scales.

My study is the first large scale approach attempting to find a relationship between the coverage of smooth brome and native herbivores species. Although I did find some interesting trends suggesting that smooth brome may have a biological affect at the two largest spatial scales all results were non-significant. I was uncertain if a lack of power at the larger spatial scales may have led to non-significant results, therefore I ran a power analysis to determine appropriate sample sizes need to find statistical significance. Based on power analyses at a significance level of 0.05 and power of 0.8 I needed a minimum of 115 prairie fragments and 72 watersheds to find a significant effect of smooth brome coverage on herbivore species richness in the models. Obtaining this high of a sample size was not feasible in this study. Given the high number of replications needed based on a power analyses there is a possibility that the invasion of smooth brome, in fact, is not altering local herbivore species RDE. Considering the uncertainty of whether smooth brome has an effect on the native herbivore community, I suggest that future research incorporate herbivore species composition and the presence of generalist predators to provide more insight into the potential changes in the resident herbivore community as the coverage of smooth brome increases. Research that accounts for species composition of specific predator, generalist and specialist herbivore species may also provide a more complete understanding between the interactions of plant invasion and their effects on arthropod communities (Gerber et al. 2008). I also suggest researchers incorporate critical landscape factors (prairie isolation, connectivity and surrounding landscape) in their studies in order to determine what factors other than invasive species may have an effect on herbivore species assemblages across spatial scales.

CHAPTER 5. SUMMARY AND CONCLUSIONS

In this dissertation, I examined the mechanisms responsible for the successful establishment, spread and ecological impacts of an invasive plant across the tallgrass prairies of the Midwestern United States. My research was separated into three different studies. In chapter 2, I used a GIS-based field survey across three prairie fragments to demonstrate the patch dynamics between a highly invasive grass *Bromus inermis* (smooth brome) and a common dominant native grass species, *Spartina pectinata* (prairie cordgrass). Chapter 2 provided data on the establishment and extinction of native plant patches in relation to the spread of an invasive species (but for exceptions see Rice et al. 2000, Huang and Zhang 2007). My results were consistent across three different prairie fragments and indicated that the invasive plant was capable of suppressing native plant growth, reducing successful establishment and increasing extinction risk as the coverage of the invasive plant increased. Although my data were observational, they provided a basis for an experimental approach (discussed in Chapter 3) to test possible mechanisms that may have driven the observed results.

In Chapter 3, I explored how germination success and interspecific competition vary across a heterogeneous landscape. Results indicate that both the native and invasive species are capable of establishing across the majority of dominant habitats commonly found in the tallgrass prairies, although these data suggest that disturbance to the plant community facilitates the invasion process when the invasive plant is colonizing from seed. These data provide further support for the hypothesis that disturbance is likely to promote invasions of non-native plants (Wiser et al. 1998, Davis et al. 2000, Larson et al. 2001, Otfinowski and Kenkel 2010). Once established I observed strong interspecific competitive interactions in which the invasive species suppressed native plant stem production and average plant height. I also found evidence that suggests environmental heterogeneity may facilitate the persistence of native cordgrass. Results from my GIS study and experimental seed manipulations suggest that native cordgrass was able to tolerate flooding and higher salinity levels than invasive smooth brome. Overall, experimental results coincide with my observational GIS study. During both studies, I observed evidence for negative growth and persistence of native species in the presence of a highly invasive grass.

For my final research chapter, I moved from exploring interactions between plant species and explored the potential impact of the spread of an invasive plant on local herbivore assemblages across multiple spatial scales. Incorporating multiple spatial scales is a critical component to understanding ecological processes but is an area in invasive plant-herbivore interactions that is rarely explored. In my herbivore survey, interesting trends suggest that effects of the invasive plant may be stronger at larger spatial scales than at small local scales (1-m^2). At the spatial scale of single prairie fragments, there was a decrease in herbivore species diversity and evenness as the percent coverage of the invasive plant increased. Simultaneously as the percent coverage of the invasive plant increased, there was a large decrease in species herbivore richness as the watershed spatial scale. Although the results were not statistically significant, they appear to be biologically important. I also found that plant species richness (only measured at the 1-m^2 spatial scale) had a positive relationship with herbivore species richness and evenness. Results also indicated that spatial factors other than percent coverage of invasive smooth brome might play a critical role in determining herbivore species assemblages.

Results from this research are not likely to be limited to the invasion of smooth brome in tallgrass prairie systems. My findings coincide with other research and help explain findings in other studies outside the tallgrass prairies. For example, Gurevitch and Padilla (2004) suggest that invasive plants are likely to cause displacement of native plant species rather than cause species extinctions, but to date, most of the evidence is correlative and it is unknown if invasive plants play a definitive causal role. This research has been able to combine observational and experimental approaches which not only confirm the prediction that invasive species are capable of displacing native species but also indicate that spatial and temporal heterogeneity in resources seem to prevent complete displacement of a native plant. This information may help bridge the gap between highly manipulated common garden/greenhouse studies and observational field studies. Although, these have provided tremendous insight, results often do not easily translate to findings in the field (Naeem et al. 2000). For example, greenhouse and observational studies have suggested that invasive plant competitive abilities are likely to be limited in physiological stressful environments. By incorporating natural heterogeneity of abiotic soil conditions into my field research, I came to the same results as Greenwood and Macfarlane (2009) who found that competitive dominance shifted from invasive *Juncus acutus* to native *J. kraussii* in high saline environments when compared to environments of low salinity. In my research, I found evidence of suppressed growth of invasive smooth brome and increased growth of native cordgrass in areas of high salinity. Certainly not all invasive plants will have a low tolerance to salinity, but incorporating natural heterogeneity into experimental studies can lead to discovery of common mechanisms that promote or inhibit plant invasions. Field experiments that account for natural environmental heterogeneity have been suggested as critical next steps in developing an understanding of patterns and processes responsible for the successful establishment and spread of invasive plant species (Fridley et al. 2007).

Smooth Brome Management

To date, several other species have been given management priority over smooth brome (e.g., *Cirsium arvense*, Canada thistle; *Euphorbia esula*, leafy spurge and *Artemisia absinthium*, wormwood) (K. Tompkins, personal communication). Currently there is a lack of intensive management of smooth brome across the tall grass prairies of the Midwestern United States, but land managers are starting to appreciate the need for active management as the growing body of literature indicates the negative impacts of smooth brome invasions (Bahm et al. 2011). Failing to actively manage for smooth brome can have dire consequences for dominant prairie plants (Blankespoor and Larson 1994, Willson and Stubbendieck 2000, Murphy and Grant 2005, Williams and Crone 2006, Dillemuth et al. 2009).

The use of prescribed fire has been successful in reducing the establishment, spread and abundance of smooth brome (Willson and Stubbendieck 2000). Wilson and Stubbendieck (2000) found that the timing of prescribed fires is critical and that fires should be conducted in early spring, when smooth brome is at the four to five leaf stages. Burning at this development stage prevents smooth brome from consuming limiting resources and flowering. If fires are conducted too early in the season, then smooth brome will regenerate growth. If fires are conducted too late in the season, it has been shown to be ineffective at reducing smooth brome abundance.

Findings from these studies reinforce the importance of prescribed fires before seeds of smooth brome mature and fall to the ground because grassland fires seldom damage seeds on the surface of the ground (Daubenmire 1968). If fires are conducted following seed dispersal then it is likely that dispersed seeds will have germinate and establish because of a reduction in competition due to a removal of competing vegetation. My research suggests that seeds that are located in areas with no vegetation (i.e. bare soil) are likely to germinate and establish. While the majority of seeds of smooth brome only disperse within 1 meter, they have been shown to disperse up to 5 meters from the edge of a patch (Otfinowski et al. 2008). Late season fires would also do little damage to smooth brome because it is a C_3 grass that goes dormant early. Therefore, smooth brome would not exhaust below ground resources by regenerating new growth until next spring. I do provide a caution to the prescribed fire approach because early spring fires have the potential to reduce the abundance of native cool season species (Engle and Bultsma 1984) which are likely a desired part of the plant community. Therefore, when using fire management as a tool to reduce abundances of smooth brome, it may be critical to monitor the response of native cool season plant species. If fire does reduce the abundance of cool season plants then use of reseeding natives may be desirable.

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Forrest Paul Dillemuth was born in Baton Rouge, Louisiana, in 1975. His interests in the natural sciences begin early in life, stimulated by his childhood time in The Boy Scouts of America. During this time, Forrest spent many weekends and summers exploring the outdoors, hiking and camping around the United States. Following graduation from high school Forrest forgot about his passion for the outdoors for about ten years. During that time, Forrest worked hard at building a career in the private sector. After about ten years, Forrest took a weekend trip into the mountains of Arkansas in the summer of 1999 where his passion for the outdoors was reawakened for the first time in about ten years. Upon Forrest’s return from Arkansas, he was motivated in a way he had never been before. This motivation gave Forrest the strength to return to his job and give his resignation to the best job he had ever had up to that point in his life. From that moment on, Forrest returned to Louisiana State University (LSU) enrolled in the Renewable Natural Resources School at LSU for the fall of 1999. From then on Forrest knew that he had a made a decision that would change his life forever. During his first semester back in college, he met Dr. Frank Rohwer who gave him some of the best advice of his life. Dr. Rohwer told Forrest no matter what you do, do not wait until you graduate college to begin getting experience in your field of studies, even if that means you have to volunteer. Forrest took Dr. Rohwer’s words to heart and asked him for a job. When Dr. Rohwer told him that he was sorry but there were no jobs available Forrest replied that it was ok and that he was willing to volunteer if need be. Dr. Rohwer replied that he was willing to accommodate a volunteer helping with waterfowl research but Forrest would have to find a way to get from Louisiana to North Dakota and that there was only two weeks of work that he could help with. Forrest managed to find a way to North Dakota and that two-week job quickly turned into fulltime work for the next three summers in the tallgrass prairies of North Dakota and southern Canada.

After a few summers, working in the prairies working with waterfowl Forrest met Dr. Jim Cronin, a new professor at LSU who also conducted his research with plant insect interactions in the tallgrass prairies of North Dakota. Dr. Cronin convinced Forrest to join his lab and help finish up research he was conducting in the prairie systems of North Dakota. During that time, Forrest began noticing how abundant the non-native species, smooth brome (*Bromus inermis*) and how this species seemed to have an impact on the birds, plants and insects in this system. Forrest's curiosity quickly turned into passion following receiving his bachelor's degree in 2003. Following graduation Forrest took that passion and turned it into his focus for his dissertation research. In the end, Forrest spent several years working to find how smooth brome affected the native plant and herbivores species in invaded prairies across North Dakota and Minnesota. Through his research, Forrest was able to draw the attention of several government agencies, non-profit organizations and private landowners. By the end of his dissertation, Forrest was able to bring awareness to a serious problem faced in the prairie systems by the invasion of smooth brome. He was also able to help provide critical information on how smooth brome spreads, what the impacts were on native communities and provide recommendations concerning how to manage this invasive species to help prevent and minimize future damage to native tallgrass prairies of the Midwest.