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POPULATION AND COMMUNITY APPROACHES TO UNDERSTANDING INVASION IN GRASSLANDS

By

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ABSTRACT

POPULATION AND COMMUNITY APPROACHES TO UNDERSTANDING INVASION IN GRASSLANDS

By

Sarah Michelle Emery

Because of concern over the economic and ecological impacts of invasive species, ecologists are interested in determining the factors that regulate the establishment and spread of new species arriving in communities. My research focuses on understanding factors that regulate the invasibility of communities, as well as factors that regulate population growth of invasive species, using a combination of field and mesocosm experiments in grassland plant communities of southwest Michigan.

In particular, I am interested in the role of dominant species in plant communities. In a field seed addition experiment at the W.K. Kellogg Biological Station, I investigated whether the identity and relative abundance of dominant species could regulate invasibility. I measured invasibility of vegetation patches dominated by one of four different species by adding seeds of 19 species common to Midwest US grasslands. I found that identity, but not relative abundance, of these dominant species altered invasibility. I followed the field experiment with an outdoor mesocosm experiment where I was able to control initial soil conditions and species richness of communities, but could vary the identity and relative abundance of the dominant species. A seed addition quantified the invasibility of these constructed communities. I again found that the identity of dominants again had strong affects on invasion. Using a structural equation model, I showed that the abundance of two species in particular had significant positive affects on community biomass and light reduction, which in turn had negative effects on invasibility in the first year of the experiment. Second year survival of invading seedlings was dependent on nitrogen availability, as well as biomass and light. There was some evidence that one dominant species in particular had additional negative effects on invasibility by some unknown mechanism.

I further explored the relationship between identity of dominant species and identity of successful invaders in both the field and mesocosm experiments by testing the hypothesis that successful invaders should be functionally dissimilar to the dominants. I used an indicator species analysis to test whether individual invader species were more closely associated with one dominant species over all others. Using broad functional groups of C3 grasses, C4 grasses, and forbs, I found very little evidence that invaders are most successful in communities dominated by a species in a different functional group.

Additionally, I have used a prairie restoration experiment at the Fort Custer Training Center in southwest Michigan to examine factors that regulate population growth of established populations of an exotic species, *Centaurea maculosa* (spotted knapweed). I examined effects of timing and frequency of prescribed fire on growth rates of knapweed. I found that annual summer burning was most effective at reducing growth rates of *C. maculosa*.

Together, my research demonstrates the importance of considering multiple factors in attempts to understand species invasions. Disturbance, species identity, and community diversity can all have important roles in regulating the establishment and spread of exotic species.

For my parents, Larry and Teresa Emery
And for Julie Mulroy, my undergraduate advisor
who started this whole thing

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TABLE OF CONTENTS

CHAPTER 6

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 1

INTRODUCTION

Background

Invasive species and their economic and ecological impacts have become a top environmental concern in recent years. In the US, invasive species are the second biggest threat to native ecosystems after habitat loss (D'Antonio and Vitousek 1992, UCS 2001), and one estimate of their cost is upwards of $140 billion per year (Pimentel et al. 2000). This concern is reflected in the tremendous increase in the number of published papers addressing a wide range of issues related to invasion biology over the past 20 years (Figure 1.1). A goal for ecologists is to unite these disparate studies under a conceptual framework that can both solve practical conservation problems, as well as contribute to the wider body of ecological knowledge. Sakai et al. (2001) outlined one such framework, presenting four steps any species must pass through to become "invasive": dispersal, establishment, spread, and ecological impact. My research focuses on better understanding the establishment and spread stages in this process. I am especially interested in addressing the universality of these processes for all species, not just non-native species.

Successful establishment of new species can be viewed from the perspective of the existing community, that is, what traits of communities make them open for new establishment. This is often referred to as the invasibility of a community, but the concept is important for more than just understanding success of invasive exotic species. Invasibility, in the broadest sense, describes the ease with which any new species establishes in a community, and so is fundamental to our understanding of succession as

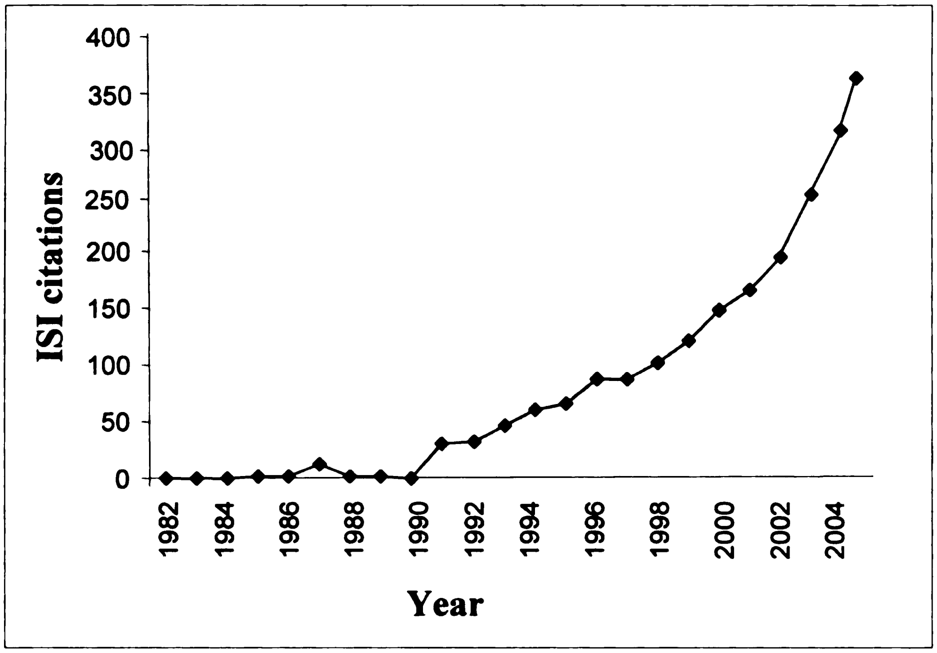


Figure 1.1. Number of papers published per year that included the search terms "invas* and ecolog*" in either the title, abstract, or keywords using the ISI citation database. Counts for 2005 are through October 15.

well as exotic species' invasions. Growing concern over the negative ecological and economic impacts of non-native species makes understanding what factors drive the invasibility of *native* communities critical (Lonsdale 1999). In contrast, understanding the invasibility of *non-native* communities may enhance the effectiveness of restoration efforts designed to facilitate planned "invasions" of degraded habitats by native species (Seabloom et al. 2003, Suding et al. 2004). More generally, increased insight into the mechanisms driving invasibility in all types of systems will inform studies of succession, community assembly, and the maintenance of community stability (Crawley 1987).

While there is considerable interest in understanding the factors that determine the invasibility of a community, they are not well resolved (Table 1.1). Specifically, I am interested in the invasibility of herbaceous plant communities as a function of diversity and resource use in those communities. Elton (1958) often is cited as the first to propose that low diversity communities are more susceptible to invasion due to more available niche space and reduced competition, though earlier work on colonization during successional processes presented similar ideas (see Davis et al. 2001). Work on the relationship between diversity and stability in the 1970s provided evidence that more diverse communities had greater stability, and therefore lower invasibility (McCann 2000). Many theoretical models also have predicted a negative relationship between diversity and invasibility based on more complete utilization of resources as diversity increases (e.g. Case 1990). However, most tests of relationships between community diversity and invasibility have focused only on the species richness aspect of diversity (e.g. Tilman 1997; Levine and D'Antonio 1999, Stohlgren et al. 1999 and 2002, Levine 2000, Naeem et al. 2000, Hector et al. 2001, Sax et al. 2002, Meiners et al. 2002). Very

Table 1.1. Literature review summary of factors related to community invasibility.

Factor	References	Relationship to Invasibility	Mechanism
Species Richness	Elton 1958, Case 1990, Drake et al. 1996, Tilman 1997, Naeem et al. 2000, Hector et al. 2001, Hodgson et al. 2002, Stachowicz et al. 2002, And many more	Negative	-Niche packing, -Resource complementarity -Sampling effects
Species Richness	Palmer and Maurer 1997, Stohlgren et al. 1999, 2002, Levine 2000, Moore et al. 2001, Meiners et al. 2002, Sax et al. 2002	Positive	-Environmental control -Habitat microheterogeneity -Facilitation
Abiotic resources (light, water, etc.)	Davis and Pelsor 2001, Foster et al. 2002, Holway et al. 2002, Kolb et al. 2002, Stohlgren et al. 2002	Positive or negative, depending on resource	-Competition for resources
Disturbance	Hobbs and Huenneke 1992, Parker et al. 1993, D'Antonio et al. 1999, Prieur-Richard and Lavorel 2000, Davis and Pelsor 2001, Lyons and Schwartz 2001, Stohlgren et al. 2002	Positive, or none	-Resource flush -Release from competitors -Open safe sites
Fluctuating Resource Availability	Davis and Pelsor 2001, Davis et al. 2000, Foster et al. 2002	Positive	-Resource availability
Scale	Lonsdale 1999, Stohlgren et al. 1999	Variable	-Abiotic factors more important at landscape scale
Functional Group Richness	Prieur-Richard et al. 2000, Symstad 2000, Dukes 2001	Negative	-Resource complementarity
Productivity	Goldberg and Werner 1983, Peart and Foin 1985, Foster and Gross 1997, Smith and Knapp 1999, Suding and Goldberg 1999, Hector et al. 2001, Lyons and Schwartz 2001	Positive, negative, or none	-Inhibit or facilitate germination and seedling establishment
Species Identity	Crawley et al. 1999, Law et al. 2000, Wardle 2001, Stachowicz et al. 2002	Usually negative	-sampling effect or strong competition from one species
Predators/ Herbivores	Knops et al. 1999, Maron and Vila 2001, Miller et al. 2002	Negative?	-Keystone effects?
Dominance/ Evenness	Robinson et al. 1995, Nijs and Roy 2000, Stachowicz et al. 2002, Wilsey and Polley 2002, Wooton 2002	Positive or negative	-Sampling effect -resource use -single species dominance

little of theory or empirical work has addressed the importance of other aspects of biodiversity for community functioning.

Recently there has been a call to acknowledge and better understand the role of other aspects of biodiversity, such as species evenness and species composition/identity (e.g., Wardle 2001, Wilsey et al. 2005). The relative abundance of species (evenness) is not necessarily predictably related to community richness (e.g. Margalef 1963, Whittaker 1965, McNaughton and Wolf 1970, Weiher and Keddy 1999), and so deserves further examination. While several recent studies have demonstrated significant effects of species identity on invasibility (e.g., Crawley et al. 1999, van Ruijven et al. 2003), it may be impossible to generalize the role of individual species identity for community functions. However, dominant species are known to exert strong influence over community dynamics and ecosystem function (McNaughton & Wolf 1970, Crawley et al. 1999, Grime 2001, Dangles & Malmqvist 2004). With my dissertation work, I focus on developing a better understanding of the role of dominant species identity and abundance in regulating the establishment of new species in grassland communities.

While insight into establishment of new species into communities can be achieved by focusing on early survival of new invaders (i.e. seedlings) (e.g., D'Antonio 1993, O'Connor 1995, Edwards et al. 2005, Yakimowski et al. 2005), a whole-population approach is often needed to understand how invaders spread (Crawley 1986, Higgins et al. 1996). Spread of established populations (i.e. positive growth rates) can be more dependent on survival or reproduction of established individuals than on survival of young individuals (e.g., Silvertown et al. 1993, Parker 2000). Further, population spread is often a function of disturbance in the system (Hobbs and Huenneke 1992, D'Antonio et al. 1999), so it becomes important to examine effects of the disturbance on various life stages of invaders. As part of my dissertation, I examine the population dynamics of one particular established invasive species, *Centaurea maculosa* (spotted knapweed) in response to prescribed fire in a prairie restoration.

Organization of the Dissertation

In this thesis, I describe my work examining plant invasions in Michigan grasslands. I use both population and community approaches to understand two different aspects of invasion: establishment and spread.

In the second chapter, I examine the effect of timing and frequency of disturbance on the population growth (spread) of a noxious invasive species, *Centaurea maculosa,* in a prairie restoration experiment at the Fort Custer Training Center (Augusta, MI). The timing and frequency of prescribed fires used in prairie and savanna restoration projects are important variables to consider because they can differentially affect the survival of individual plant species present, as well as whole-community responses. I used population matrix analysis to evaluate the demographic consequences of burning on populations of the invasive species. I found that annual summer burning was the only treatment that significantly reduced overall population growth rates. The summer burn treatments reduced population growth by reducing reproduction. In general, reproduction of adults as well as survival of non-reproductive adults and juveniles remained important in all treatments. This indicates that future attempts to control *C. maculosa* should focus on combinations of treatments targeting these life stages.

In the third and fourth chapters, I examine aspects of invasibility of intact oldfield plant communities at two sites near the W.K. Kellogg Biological Station of Michigan State University (Turkey Meadow/Louden Field and Lux Arbor, see site descriptions below). I added seeds of 19 different species to vegetation patches within the fields that differed in dominant species and resource availability. In the third chapter, I address the questions: 1) Does the identity of the dominant species affect invasibility? and 2) Does the relative abundance of the dominant affect invasibility? I compared any effects of dominant species with effects of other factors such as community species richness and biomass. Independent of community species richness and measured abiotic variables, I found that the identity of the dominant species affected invasibility. The abundance of dominants was rarely a significant predictor of invasion. Species richness was the only other significant predictor of invasion, and was usually positively related to invasibility. These results suggest that dominant species identity may be as important as species richness in determining invasibility in grassland communities.

In the fourth chapter, I implemented a controlled experiment using constructed grassland communities ("mesocosms") with equal species richness, but different identities and relative abundances of dominants to examine the relationship between community evenness, composition, and invasibility. I added seeds of the same 19 species used in the field experiment to these communities to quantify invasibility. There were no consistent relationships between invasibility and evenness among the different dominant treatments; again I found that the identity of the dominant species had significant effects on invasion. These effects could be partitioned into indirect effects through changes in resource levels, especially light, and direct effects that were due to some unmeasured mechanism. The differences in invasibility among plots with different dominant species were equal or greater in magnitude to the differences due to species richness reported in other studies.

In the fifth chapter, I examine relationships between the identity of successful invaders and the identity of community dominants in both the field and mesocosm experiments. I asked the question: Are invaders that are functionally dissimilar to the dominant species more likely to succeed than other species? I also examined whether non-native species were more likely to invade than native species, and whether native-dominated communities were more resistant to invasion than non-native dominated communities. Limiting similarity theory offers the prediction that successful invaders should be functionally different from species already in the community. Because dominant species are known to have strong effects on ecosystem functioning, I hypothesized that successful invaders should be functionally dissimilar from community dominants. In both experiments, I found that while a few invader species showed differential success across communities these invaders did not necessarily have highest success in plots with functionally different dominants. Indeed, most species showed no variability in success in relation to the identity of the dominants, suggesting that results from experiments using a single species of invader should be interpreted with caution.

In the final chapter, I give a general summary of my dissertation and present a possible future research direction, examining the effects of mutualisms on invasibility of communities.

Site Descriptions

The experiment described in chapter two was established as part of a larger restoration study examining whole-community responses to different management regimes (see Gross and Suding 2002 for details) at the Fort Custer Training Center (Calhoun County, MI), a US Army National Guard base with approximately 3000 ha of undeveloped, mostly forested, land near Augusta, Michigan, USA. The area was in agriculture from the 1850s until the 1930s, when it became part of the Fort Custer military base. Annual rainfall in this area averages 86-91cm. Soils consist of sand and sandy loam glacial outwash deposits. The locations of my four study sites within the FCTC are shown in Figure 1.2.

The field seed-addition invasibility experiment described in chapters three and five was conducted in two oldfield sites near the W.K. Kellogg Biological Station in southwest Michigan (Figure 1.3a). Lux Arbor Reserve (Barry County, MI) was donated to Michigan State University in 1991 by Dr. Richard and Mrs. Irmgard Light. The 1300 acre property contains areas of active row-crop agriculture and conifer plantations, as well deciduous woods, wetlands, oldfields, and ponds. I used a 15ha oldfield located within the Lux Arbor Reserve (Figure 1.3b, 42.2833°N, 85.2768°W), that had been abandoned from agriculture for approximately 25 years. Occasional mowing was the only management in the years before implementation of this experiment. The second site for this study was located in Turkey Meadow and Louden Field (42.2478°N, 85.2366°W; 42.2461°N, 85.2316°W, Figure 1.3c), adjacent oldfields on the KBS main site which has not been cultivated since 1960. The soil at all these sites is Kalamazoo sandy loam (Burbank and Gross 1992).

The mesocosm experiment described in chapters four and five was conducted outdoors at the KBS Field Lab (42.2460°N, 85.2359°W; Figure 1.3a).

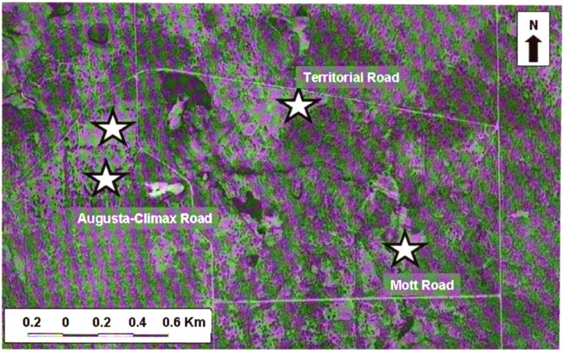


Figure 1.2. Aerial photograph (Photo source: Earthdata International, April 16, 2001. NAD 83) of the experimental sites at Fort Custer Training Center, Augusta MI. White stars indicate the four sites used in this study.

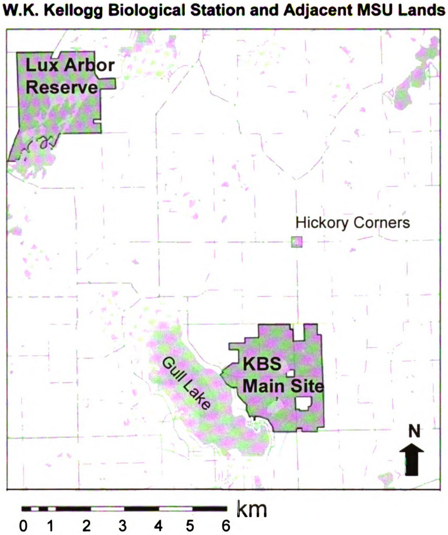
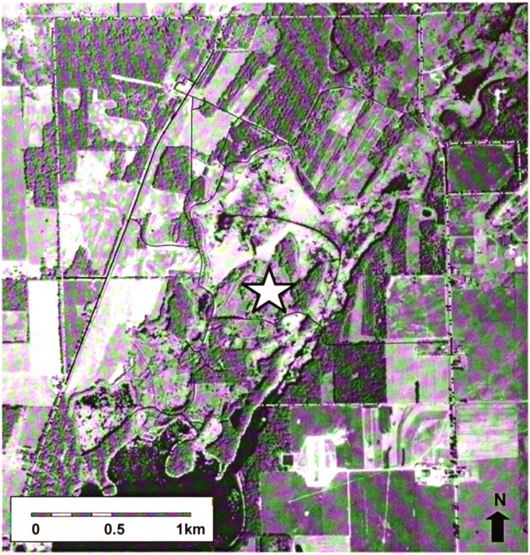


Figure 1.3a. Regional map of the W.K. Kellogg Biological Station and Lux Arbor Reserve.

http://lter.kbs.msu.edu/GIS/Aerial%20Photo/Aerial%20Photography.html

Figure 1.3b. Aerial photograph of the KBS main site (source: Abrams Aerial Survey Corp. May 7, 1993). Locations of experiments are indicated by white stars.



http://lter.kbs.msu.edu/Maps/Thematic/Figure9.htm

Figure 1.3c. Aerial photograph of Lux Arbor Reserve (August 2003). Location of experiment indicated by white star.

CHAPTER 2

Emery, Sarah M., and Katherine L. Gross. 2005. Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed *Centaurea maculosa*. *Journal of Applied Ecology* 42: 60-69.

CHAPTER 2

EFFECTS OF TIMING OF PRESCRIBED FIRE ON THE DEMOGRAPHY OF AN INVASIVE PLANT, *CENTAUREA MACULOSA* SPOTTED KNAPWEED.

Abstract

1. Prescribed burning is a key tool used in prairie and savanna restoration projects. The timing and frequency of prescribed fires are important variables to consider because they can differentially affect the survival of individual plant species present, including noxious exotic species.
2. We used annual censuses and population matrix analysis to evaluate the demographic consequences of burning on populations of the invasive species, *Centaurea maculosa* spotted knapweed, in a Michigan USA prairie restoration experiment. We compared spring, summer, and autumn burns at two frequencies: annually (2000-20003) or in alternate years (2001, 2003). We examined the effects of different seasons and frequencies of prescribed fire on the survival, growth, and reproduction of *C. maculosa* populations, and used life table response experiments and elasticity analyses to determine how season of fire affects population growth rates.
3. We found that annual summer burning was the only treatment that significantly reduced overall population growth rates.
4. The Life Table Response Experiment Analysis indicated which life stages contributed the most to changes in population growth rates under the different treatments. The summer burn treatments reduced population growth by reducing reproduction.
5. The different burn treatments altered the elasticity structure of populations, but in

general, reproduction of adults as well as survival of non-reproductive adults and juveniles remained important in all treatments. This indicates that future attempts to control *C. maculosa* should focus on combinations of treatments targeting these life stages.

5. *Synthesis and applications:* Management decisions regarding prescribed fire options in grassland restoration projects should consider the responses of individual species already present in the system. In particular, it is important to consider the effects of burning on noxious invasive species that may or may not have different life histories and responses to fire when compared to native species. Population matrix modelling provides a more complete picture of effects of management on population responses, as compared with other measures based only on community composition or relative abundance. Depending on the goals of a restoration, non-traditional management options, such as summer burning in Midwest USA prairies, may be effective management tools for the control of invasive species.

Introduction

Biologists and land managers often use prescribed burning as a key tool in prairie and savanna restoration projects because of the historical dependence of these systems on fire (Axelrod 1985). Depending on the goals of a restoration project, the timing and frequency of prescribed burns are important variables to consider in grassland restoration because they can differentially affect individual plant species responses (Howe 1995; Gillespie & Allen 2004). In the Midwestern USA, managers often use spring burning to stimulate growth of desirable warm season native grasses, but if control of invasive species is a goal of a restoration project it is important to recognize that invasive and native species do not always respond similarly to fire. In a review of studies using prescribed fire to control invasives, D'Antonio (2000) found that in eighty percent of studies, prescribed burning either increased, or had no effect on, invader abundance.

Evidence suggests that the effects of fire on species of concern often depend on when the burning occurs relative to the species' life cycle and overall community phenology (e.g. Enright & Lamont 1989; Brewer & Platt 1994; Lesica 1999). For example, summer fire in California grasslands effectively controls yellow starthistle *Centaurea solstitialis* L. because this plant grows and reproduces after earlier-flowering native species have dispersed seeds (DiTomaso, Kyser & Hastings 1999). In contrast, summer burns in Midwest USA grasslands can enhance growth of unwanted quackgrass *Agropyron repens* (L.) Beauv., by reducing litter and suppressing late-season competitors (Howe 1995). For smooth brome *Bromus inermis* Leyss., burning in the spring during tiller emergence either increased abundance or had no effect, while later season burns during tiller elongation and flowering had a negative effect on biomass (Willson 1997).

Fire frequency can also be an important management consideration. Annual burns often have very different effects on native species abundance than less frequent burn regimes (e.g. Gross, Frost & Morris 1998; Hoffman 1999; Morgan 1999; Brewer 2001). Exotic species also respond to variation in fire frequency. For example, a study in West Africa showed that annual fire helped control an exotic grass, but less frequent fire actually increased population stability through accelerated nutrient cycling (Garnier & Dajoz 2001).

Many studies only consider short-term responses of specific life-stages in evaluating the efficacy of management treatments (e.g. Maret & Wilson 2000; MacDonald *et al.* 2001). Basing decisions on the effects of a management treatment on a single life stage or community property, such as seedling recruitment, adult abundance, or relative aboveground biomass, can lead to incorrect assumptions about whole-population responses and ineffective management practices (Freckleton 2004). For example, fire increased adult mortality of an invasive grass in Venezuelan savanna, but also increased seed germination and seedling growth, actually promoting spread of the invader (Baruch & Bilbao 1999).

Modelling approaches that account for the responses of all life stages of a species can better assess the effects of management regimes, such as prescribed fire, on populations of a target species (e.g. Caswell & Kaye 2001; Kaye *et al.* 2001; Rees & Hill 2001; Buckley *et al.* 2004). Transition matrix models are one useful tool in evaluating management options because they give a good picture of whole population responses and integrate treatment effects on all life history stages (Schemske *et al.* 1994; Horvitz & Schemske 1995).

In this study, we used transition models to evaluate the effects of prescribed burns on populations of spotted knapweed *Centaurea maculosa* Lam., an invasive forb that is problematic in grasslands of the Western and Midwestern United States (Sheley, Jacobs & Carpinelli 1998). We examined effects of spring, summer, and autumn burning, either annually or in alternate years, on *C. maculosa* populations in an experimental restoration project located in degraded prairie remnants in southwestern Michigan, USA.

Results from transition matrix models showed that frequency and season of burn had different effects on spotted knapweed population growth.

Methods

The Focal Species

Centaurea maculosa spotted knapweed is one of the most problematic invasive species in North America, infesting nearly 1.5 million ha of rangeland in the Western USA (Mauer, Russo & Evans 1987), and also invading oldfields and prairie remnants in the Midwestern USA. Native to Europe, this species was introduced to the USA in the 1890s through contaminated *Medicago sativa* L. alfalfa seed. In the Western USA, *C. maculosa* has been known to form monocultures in previously grass-dominated rangeland, leading to altered nutrient cycling and desertification problems (Rice *et al.* 1997) as well as loss of economically important grazing areas. *Centaurea maculosa* is also spreading throughout the Midwestern USA, and is common along roadsides, lower productivity prairie and savanna grasslands, and Lake Michigan sand dunes (S. Emery, personal observations). Most control efforts for *C. maculosa* have focused on large-scale herbicide applications or biocontrol efforts (e.g. Rice *et al.* 1997; Callaway, DeLuca & Belliveau 1999). In Midwestern prairie remnants, prescribed fire is often used as a tool to control *C. maculosa* and other non-native species while encouraging growth of native species. However, data to support fire as a successful management tool for *C. maculosa* are sparse.

Centaurea maculosa is a short-lived, usually iterocarpic, perennial forb which can live up to eight years. Seedlings germinate in late autumn or early spring and usually remain as juvenile rosettes for their first year. After the first year, individuals can bolt and flower in late summer, dispersing seeds throughout the autumn. In subsequent years, individuals can continue to bolt and reproduce, or can revert to a vegetative (non-reproductive) adult rosette. Older plants can have multiple rosettes and multiple bolting stems. In our sites, individuals produce between 10 and 1100 seeds per year (S. Emery, unpublished data). *Centaurea maculosa* seeds are capable of remaining viable in the soil for up to 8 years in Montana (Davis *et al.* 1993), although the generality of these findings to other locations is not established. In Michigan populations, a viable seedbank persists for at least one year (see below).

Study Site

This experiment was established as part of a larger restoration study at the Fort Custer Training Center (FCTC), a US Army National Guard base with approximately 3000 ha of undeveloped, mostly forested, land near Augusta, Michigan, USA. Historically, this landscape was a patchwork of prairie, oak savanna, and forest communities maintained by natural summer fires, and spring and autumn fires used by Native Americans (MDMVA 2001). Currently, this site is mostly second growth deciduous forest intermixed with small prairie and oak savanna remnants. Dominant native species in these remnants include goldenrod *Solidago spp.*, poverty oatgrass *Danthonia spicata* (L.) Beauv, and little bluestem *Schizachyrium scoparium* (Michx.) Nash. Common non-native species in these sites in addition to *C. maculosa* include hawkweed *Hieracium caespitosum* Dumort., sheep sorrel *Rumex acetosella* L., and Kentucky bluegrass *Poa pratensis* L. The area was in agriculture from the 1850s until the

1930s, when it became part of the Fort Custer military base. Annual rainfall in this area averages 86-91cm. Soils consist of sand and sandy loam glacial outwash deposits.

Experimental Design and Treatments

From April 2000 to October 2003, we conducted a replicated experiment on four prairie remnants within the FCTC to look at the effects of alternative fire management on *C. maculosa* demography. These remnants varied in primary productivity (136-508 g/m^2) and spotted knapweed abundance (6-25% of total biomass). We established seven burn treatments in 5x5m plots at each of the four sites. Burn regimes included annual and alternate year spring (April), summer (July), and autumn (October) burns, along with a control (no burning). We initiated the annual burns in 2000 and burned these plots every year (through 2003); the alternate year burns occurred in 2001 and 2003. We used a propane tank and torch to start fires along one edge of the plot that then carried across the entire plot. In some years, productivity and fuel loads were too low to carry a fire, so we used the torch across the entire plot to assure a complete burn. We collected pre- and post-burn biomass from 0.50 m x 0.25 m areas outside of our sampling plots to estimate fire intensity. All fires were of relatively low intensity (consuming 40-57% of total biomass) and typically had flames 8-20cm high. The intensities of these small experimental fires were comparable to larger scale prescribed fires in adjacent natural areas (S. Emery, unpublished data), especially in the first few years. In 2003, one of our experimental sites was accidentally burned by the FCTC managers, so our demographic analyses for 2003 are based only on three sites. While the whole community response to experimental burning was evaluated as part of the larger study (Gross & Suding 2002;

Suding & Gross, unpublished data), here we specifically focus on the demographic responses of *C. maculosa* populations to the burning treatments.

Censuses and life cycle components

We established a 1m x 0.25m permanent census plot in each of the larger treatment plots and marked all *C. maculosa* individuals with unique identifier tags, recording life stages of all marked individuals in the autumns of 2001, 2002, and 2003. Approximately 650 individuals were marked and followed through the three years. Individuals were classified either as first-year juveniles, non-reproductive adults, one-stemmed small adults, or multi-stemmed large adults. We also censused newly emerged seedlings in autumn and spring of these years. We quantified reproduction for all bolting individuals by counting all seeds produced per individual in autumn 2002; in 2001 and 2003, we estimated reproduction by counting seed heads on each individual and multiplying these values by the average number of seeds per head (from 2002 data). In 2002, we estimated recruitment from the seedbank by placing seed-exclosure cages over plots to the side of the permanent census plots in early August to prevent dispersal of seeds produced in that year into these plots. The cages were approximately 0.25 m x 0.25 m x 0.10 m and constructed from 6.0 mm hardware cloth, lined with bridal veil to catch dispersing seeds. We emptied the cages of seeds and debris weekly, so that light would be minimally obstructed. Cages were left on the ground until the autumn census in October. Seedling emergence in these plots was assumed to be from seeds in the seed bank. We were unable to quantify seed longevity in the seedbank in this study, so we used other published seedbank data for *C. maculosa* (Davis *et al.* 1993) where approximately half of seeds in the seedbank were no longer viable after one year. All census values were log-transformed (ln(x+1)) before analysis.

In 2001, we determined if the fire treatments affected phenology of *C. maculosa* populations by conducting weekly censuses of the number and stage of flowers per individual in separate marked plots. Stages included buds, open flower heads, senescing flower heads, and mature seed heads.

We harvested aboveground biomass in July of 2001 and 2002 in $0.25m^2$ plots outside the census area, dried and weighed the biomass, and sorted to species to quantify the effects of the burns on the relative abundance of *C. maculosa* in the community.

We used general linear models (SAS Institute, Inc. 1999-2001, PROC GLM) with planned contrasts between treatments and the control (no burn) to test for treatment effects on census, phenology, and biomass data.

Analyses: Matrix projections

We constructed stage-based (Lefkovitch) transition matrices for populations in each treatment at each site for each year (2001-02 and 2002-03). Despite differences in site productivity and initial abundance of *C. maculosa*, site was never a significant predictive factor of growth rates (for 2001-02 transitions: $F_{3,32}=1.6$, $P=0.22$; for 2002-03 transitions: $F_{2,24}=0.42$, $P=0.66$), so we averaged across sites for all analyses presented here. We also calculated summary matrices for each treatment across both years by weighting each transition by its frequency in the population. These summary matrices better represent the dynamics over the two years of observations. We used five stages in the model: seedbank, first-year juveniles, non-reproductive adults, small reproductive adults, and large reproductive adults (Figure 2.1). Survival, growth, and regression (transition to a smaller stage class) were calculated by following the fates of tagged individuals. Reproduction was represented as the number of first-year juveniles appearing every year (minus the small number of juveniles appearing in the seed exclosure cages in 2002, which we used to measure transitions from the seedbank). Transitions were calculated from seed production fractions (e.g. a plant that produced 10% of the total seeds in a plot was assumed to account for 10% of the total first-year juveniles per plot). Contributions to the seedbank were calculated based on total seed production minus the seedlings that germinated. This is probably an overestimation of contributions to the seedbank, as we did not account for seed predation or other sources of seed death. Contributions from the seedbank were calculated from germination in our seed-exclosure cages. We assumed a 50% survival rate of seeds in the seed bank from year to year because we were unable to directly assess effects of fire on survival of seeds in the seedbank.

We calculated the dominant eigenvalue for each transition matrix using Matlab 6.1 (MathWorks 1994-2004) to determine population growth rate, λ. We compared growth rates across treatments using planned contrasts in a general linear model to quantify effects of burn regimes on overall demographic success (Horvitz & Schemske 1995).

We also compared actual stage distributions observed in 2003 with projected stable stage distributions (calculated as the right eigenvector of the summary matrix for

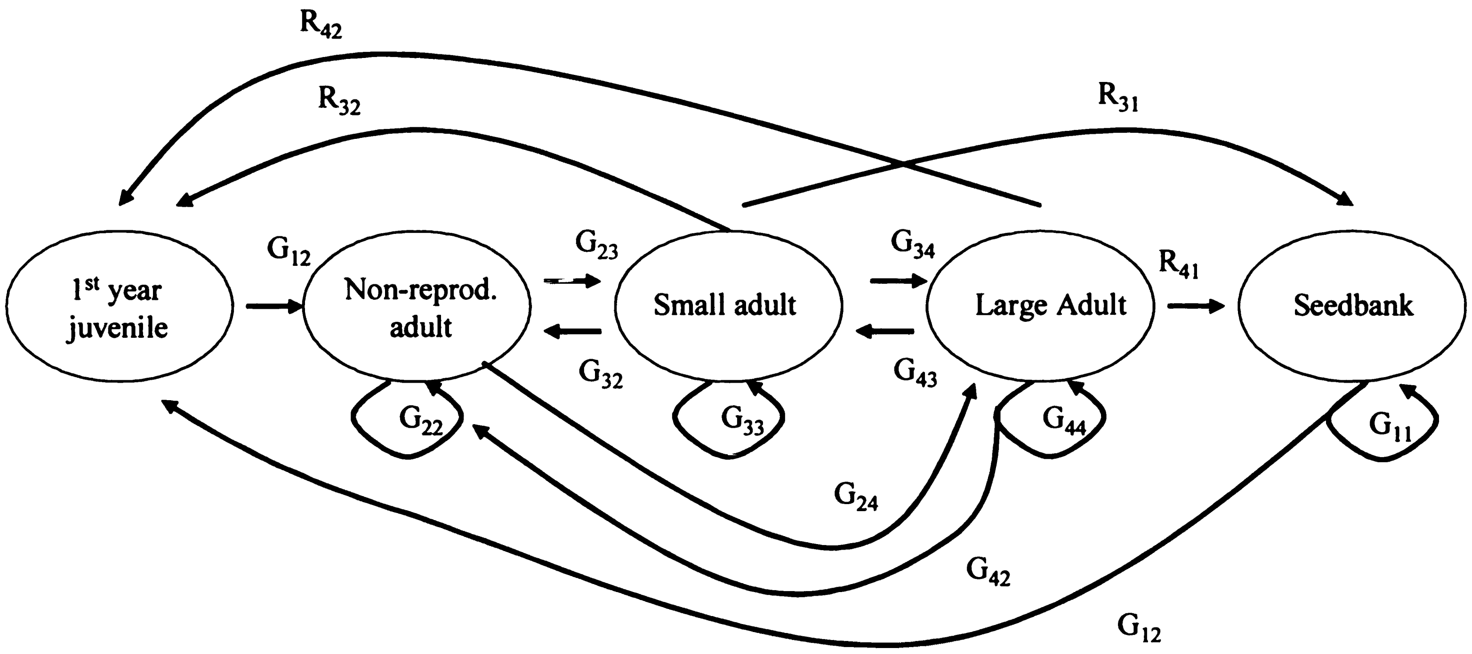


Figure 2.1. Life cycle graph of *Centaurea maculosa*. G transitions indicate growth, survival, or regressions.

R transitions indicate reproduction.

each treatment) using a Pearson chi-square test. For these analyses, we used the projected stable stage distribution as the expected value and the stage distribution observed in the field as the observed value, in order to estimate the accuracy of the population growth rate predictions for the populations. If actual stage distributions vary significantly from projected stable stage distributions, the validity of calculated population growth rates assuming asymptotic dynamics is questionable, although, in at least one case, Caswell & Werner (1978) showed that within ten years, transient and asymptotic dynamics can be strongly correlated.

For all matrix analyses, we assumed no explicit density dependence. While density dependence can play important regulatory roles in population dynamics (e.g. Buckley *et al.* 2001; Freckleton *et al.* 2003; Blundell & Peart 2004), our data collection methods did not allow for explicit incorporation of density dependence in our models.

Life Table Response Experiment

We compared effects of treatments on each life stage by performing a Life Table Response Experiment (LTRE) analysis (Horvitz *et al.* 1997; Ehrlén & Van Groenendael 1998, Hoffman 1999). LTRE is a retrospective analysis that discerns how treatments affect population growth by examining effects of treatments on individual transitions. It involves a comparison of sensitivities for each matrix transition with the actual magnitude of change caused by treatments to examine impacts on population growth rates so that:

$$\mathrm{LTRE}_{ij} = \Delta x_{ij} \times \delta\lambda/\delta x_{ij} \big|_{\mathrm{mean}}$$

Where Δx_{ij} is the difference between the treatment and control (no burn) for a given transition parameter, x_{ij} and $\delta\lambda/\delta x_{ij}\,|_{mean}$ is the intermediate sensitivity between the treatment and control matrices. LTRE makes it possible to identify mechanisms of change for each treatment instead of just summarizing overall changes.

Elasticities

We performed elasticity analyses on all summary matrices. Elasticity analysis is a prospective analysis that indicates which life cycle transitions will have the greatest proportional effects on population growth rates if changed by small amounts (Horvitz & Schemske 1995; Caswell 2001). We categorized all transitions into life stages (seedbank, first-year juveniles, non-reproductive adults, small adults, large adults, and general reproduction (seedlings)) and added elasticity values for each transition within each life stage category to calculate elasticity values for the entire life stage. For example, growth, stasis, and regression transition elasticities for small adults were added to estimate an elasticity value for the small adults' class. This analysis is often used to make decisions as to which life stage to target for management of threatened species (see de Kroon, Van Groenendael & Ehrlén 2000 for examples). However, elasticities only address changes in λ based on small changes in transition probabilities. Many management efforts cause large changes in transitions, for example reducing reproduction by 50%, and such large effects are usually outside the interpretations of elasticities (Horvitz *et al.* 1997; Caswell 2000). However, elasticity analysis can still be used as a guide in developing management efforts because it indicates potentially sensitive life stages.

Results

Population structure, phenology, and reproduction

The biomass harvests in 2001 and 2002 showed no significant effect of burning on the relative abundance (in aboveground net primary productivity) of *C. maculosa* (Figure 2.2; for 2001: $F_{5,18}$=1.14, P=0.38; for 2002: $F_{5,32}$=1.32, P=0.29).

Our monitoring in 2001 showed that there were significant differences among burn treatments in flowering phenology. Annual and alternate year spring burns significantly reduced by approximately 50% the percentage of adults that flowered ($F_{1,12}$=8.05, 14.2; P=0.009, 0.001, while annual and alternate year summer burns reduced flowering almost entirely in those populations during a burn year ($F_{1,12}$=43.6, 41.6; P<0.0001, 0.0001). Both annual and alternate year autumn burns had no effect on flowering ($F_{1,12}$=0.015, 0.40; P=0.9, 0.53) (Figure 2.3). Because of the strong effect of burning on flowering, annual summer burning reduced total reproduction (seeds) to almost zero in all years, though the reduction was not significant in 2003 (2001: $F_{1,12}$=61.2, P<0.0001; 2002: $F_{1,12}$=4.94, P<0.0001; 2003: $F_{1,12}$=1.09, P=0.29). Alternate summer burns reduced reproduction in the year of the burn in 2001, but not in 2002 or 2003 (2001: $F_{1,12}$=74.1, P<0.0001; 2002: $F_{1,12}$=0.08, P=0.93; 2003: $F_{1,12}$=0.7, P=.49). Spring burning only reduced reproduction in the alternate year burned plots in 2001 ($F_{1,12}$= 4.63; P=0.04), but only to about half the reproductive output of the control plots (Table 2.1). There was no effect of spring burning in the years following. Autumn burning never had an effect on reproduction.

Burning every summer reduced total numbers of *C. maculosa* by 4-8 times compared with the control. These plots had significantly fewer individuals than the

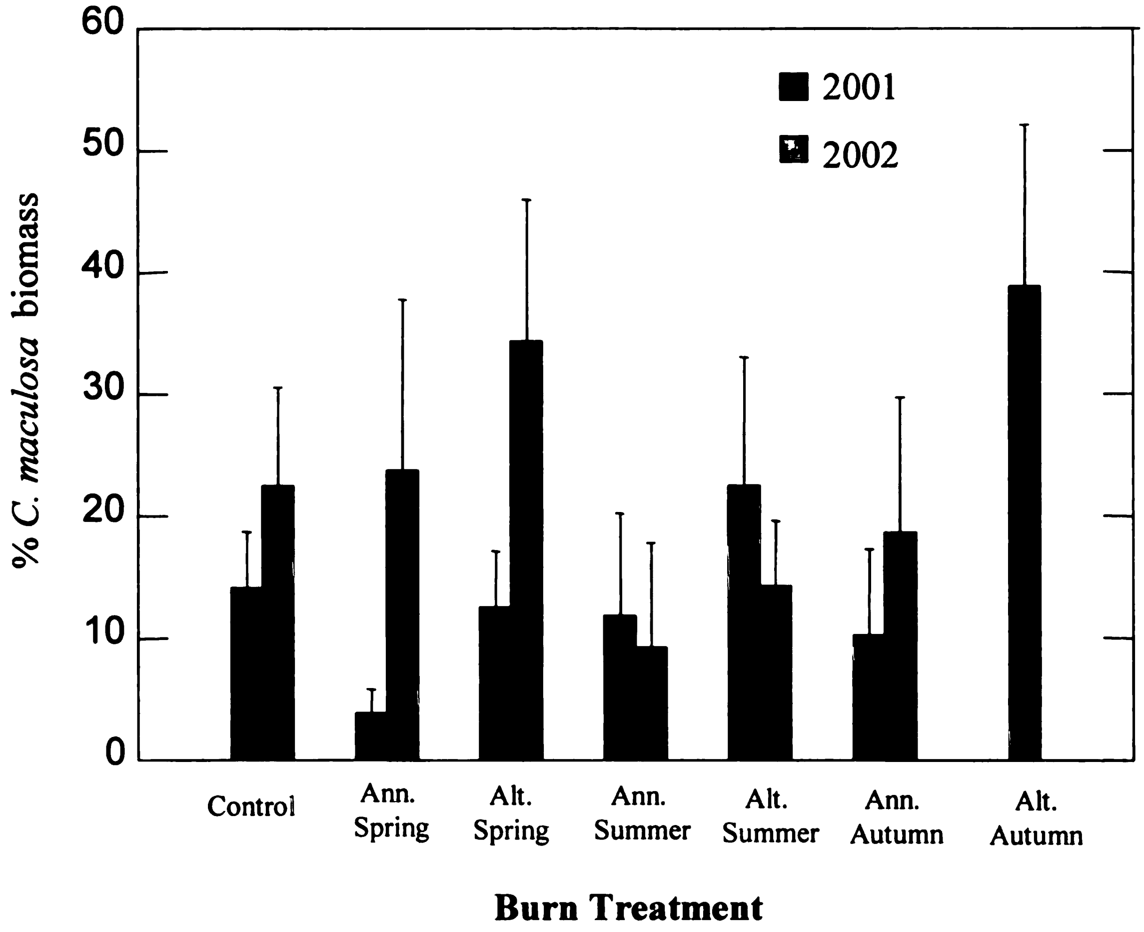


Figure 2.2. Relative abundance of *C. maculosa* (percentage of total biomass) across burn treatments in 2001 and 2002. Alternate autumn burning is not represented in 2001 because the biomass harvest occurred before the autumn burn.

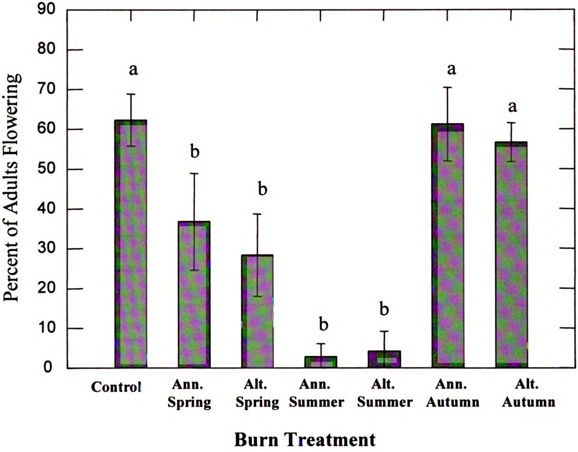


Figure 2.3. Percentage of adults flowering in 2001. Different letters indicate significant differences at *P*=0.05. Error bars represent one SE of mean.

Table 2.1. Average number of juveniles, non-reproductive adults, small adults, large adults, and seeds per 0.25m^2 for each treatment for each year. Asterisks indicate significant differences (**P=0.01, * P =0.05, $^{\S}P$ <0.10) from control values.

Year	Treatment	# Juveniles	# non-reproducing adults	# small adults	# large adults	Total # of plants	Seed Production
2001	Control	11.13	1.38	2.25	1.63	16.4	147.5
	Annual Spring	6.75	2.00	1.00	1.50	11.3	83.5
	Alternate Spring	17.25	0.75	1.50	1.50	21.0	60.1*
	Annual Summer	2.50	0.00	1.00	1.25	4.8*	1.2**
	Alternate Summer	5.25	0.50	2.25	2.50	10.5	0.0**
	Annual Autumn	7.50	0.25	1.00	0.50	9.3	192.8
	Alternate Autumn	10.75	0.25	3.50	1.00§	15.5	311.8
2002	Control	11.00	8.00	4.50	2.38	25.9	512.8
	Annual Spring	10.00	6.50	2.25	1.50	20.3	439.8
	Alternate Spring	5.25	9.50	6.25	2.25	23.3	535.8
	Annual Summer	0.25**	2.50	1.00*	1.00	4.8*	19.3*
	Alternate Summer	2.75§	3.75	3.00	3.25	12.8§	644.3
	Annual Autumn	7.75	5.25	1.25*	1.00	15.3	295.8
	Alternate Autumn	12.00	7.00	3.75	3.25	26.0	800.3
2003	Control	5.33	12.67	4.00	2.67	24.7	346.0
	Annual Spring	2.00	14.33	2.00	1.00	19.3	211.5
	Alternate Spring	2.67	10.00	3.33	3.33	19.3	269.1
	Annual Summer	0.00**	0.67**	1.67	0.67	3.0**	201.9
	Alternate Summer	1.67	4.33§	1.67	3.67	11.3	83.3
	Annual Autumn	2.00§	9.00	0.33§	1.33	12.7	70.5§
	Alternate Autumn	2.33	6.00	5.67	3.33	17.3	413.3

control plots every year of this study (2001-03) (2001: $F_{1,12}=2.15$, $P=0.04$; 2002: $F_{1,12}=2.18$, $P=0.04$; 2003: $F_{1,12}=2.73$, $P=0.01$) (Table 2.1). When individuals were classified into stages, annual summer burning significantly reduced first-year juvenile abundances in 2002 and 2003 ($F_{1,12}=3.08, 3.21$; $P=0.005, 0.005$), reduced non-reproductive adult abundance in 2003 ($F_{1,12}=2.92$, $P=0.01$), and reduced small adult abundances in 2002 ($F_{1,12}=2.27$, $P=0.03$). Large adult abundance was not significantly reduced in any of the burn treatments ($P>0.20$ for all treatments). No other burn treatments showed significant reductions in *C. maculosa* abundances in any year.

By 2003, population stage distributions in most treatments were not significantly different from the estimated stable stage distribution (Figure 2.4), indicating that calculated population growth rates present an accurate picture of demographic success.

Population growth rates

We calculated population growth rates of *C. maculosa* in each treatment for 2001-02, 2002-03, and for the weighted mean matrices for each treatment (see Table 2.2 for details). Annual summer burning is the only treatment that significantly reduced *C. maculosa* population growth rates below 1.0 when compared to the control (for 2001-02, 2002-03, and weighted matrix: $F_{1,12}=2.14, 2.26, 2.08$; $P=0.04, 0.04, 0.06$) (Figure 2.5). Average population growth rate in the control was 1.17, indicating positive population growth, while the average growth rate in the annually summer burned plots was approximately half that (0.56), indicating population decline.

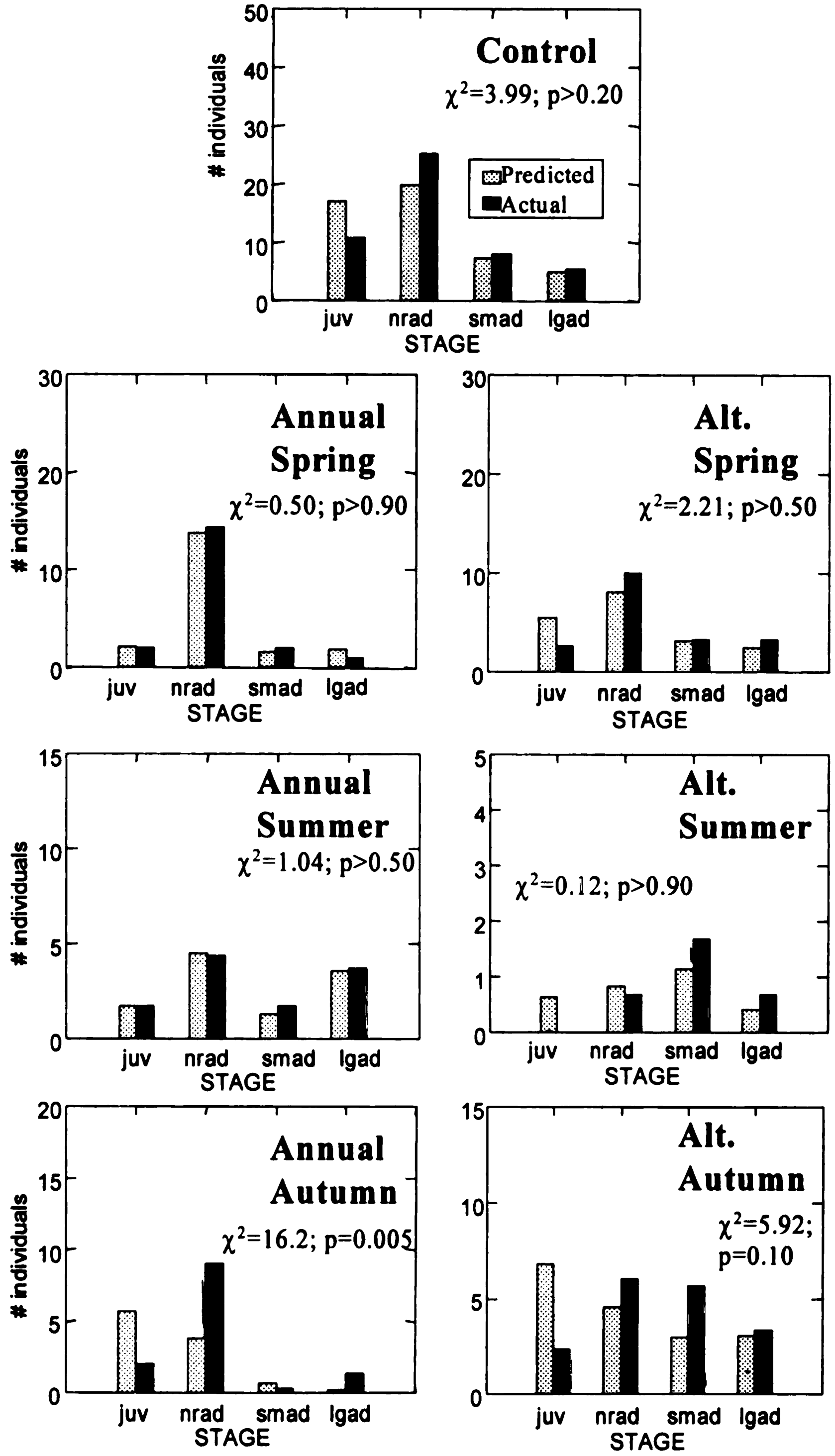


Figure 2.4. Comparison of the average observed and predicted stage distribution for each treatment in 2003. Life stages include: juvenile (juv), non-reproductive adult (nrad), small reproductive adult (smad), and large reproductive adult (lgad).

Table 2.2. Matrix transition values for weighted mean matrix for each treatment (averaged over two years and three sites). Standard deviations are in parentheses. See Figure 2.1 for transition identities.

2001-03	**Management Treatment (frequency and season of burn)**						
Transition	**Control**	**Annual Spring**	**Alternate Spring**	**Annual Summer**	**Alternate Summer**	**Annual Autumn**	**Alternate Autumn**
G_{11}	0.500 (0.00)	0.500 (0.00)	0.500 (0.00)	0.500 (0.00)	0.500 (0.00)	0.500 (0.00)	0.500 (0.00)
G_{12}	0.010 (0.013)	0.047 (0.080)	0.004 (0.005)	0.000 (0.00)	0.001 (0.002)	0.000 (0.00)	0.012 (0.016)
G_{23}	0.560 (0.151)	0.713 (0.047)	0.457 (0.240)	0.530 (0.503)	0.590 (0.365)	0.537 (0.343)	0.503 (0.055)
G_{24}	0.187 (0.162)	0.089 (0.038)	0.313 (0.142)	0.467 (0.503)	0.213 (0.201)	0.020 (0.035)	0.287 (0.185)
G_{25}	0.013 (0.015)	0.000 (0.00)	0.000 (0.00)	0.000 (0.00)	0.000 (0.00)	0.000 (0.00)	0.007 (0.012)
G_{33}	0.410 (0.151)	0.640 (0.275)	0.393 (0.267)	0.530 (0.00)	0.230 (0.398)	0.640 (0.288)	0.093 (0.162)
G_{34}	0.273 (0.078)	0.207 (0.184)	0.210 (0.252)	0.467 (0.503)	0.023 (0.040)	0.070 (0.113)	0.263 (0.237)
G_{35}	0.123 (0.061)	0.030 (0.052)	0.103 (0.146)	0.007 (0.115)	0.470 (0.476)	0.070 (0.115)	0.047 (0.081)
G_{43}	0.253 (0.153)	0.330 (0.335)	0.167 (0.144)	0.113 (0.196)	0.137 (0.118)	0.083 (0.144)	0.177 (0.166)
G_{44}	0.173 (0.115)	0.110 (0.191)	0.087 (0.090)	0.113 (0.196)	0.070 (0.121)	0.000 (0.00)	0.123 (0.108)
G_{45}	0.270 (0.120)	0.003 (0.006)	0.330 (0.144)	0.017 (0.001)	0.230 (0.252)	0.583 (0.520)	0.543 (0.396)
G_{53}	0.270 (0.127)	0.000 (0.00)	0.097 (0.167)	0.167 (0.289)	0.050 (0.087)	0.000 (0.00)	0.067 (0.115)
G_{54}	0.200 (0.200)	0.000 (0.00)	0.177 (0.154)	0.057 (0.098)	0.027 (0.046)	0.000 (0.00)	0.000 (0.00)
G_{55}	0.330 (0.153)	0.487 (0.430)	0.310 (0.271)	0.363 (0.318)	0.397 (0.356)	0.627 (0.289)	0.493 (0.503)
R_{41}	12.20 (9.23)	9.97 (8.81)	19.14 (18.13)	0.00 (0.00)	9.43 (8.95)	5.03 (8.72)	22.50 (3.95)
R_{42}	1.04 (1.18)	0.243 (0.21)	0.363 (0.123)	0.000 (0.00)	0.110 (0.105)	0.417 (0.722)	1.29 (1.01)
R_{51}	27.40 (6.68)	40.20 (37.1)	34.20 (42.09)	24.10 (41.74)	37.97 (42.07)	47.80 (32.98)	97.50 (140.62)
R_{52}	3.87 (5.21)	0.550 (0.79)	0.990 (0.884)	0.830 (1.61)	0.310 (0.285)	2.36 (2.41)	0.570 (0.981)

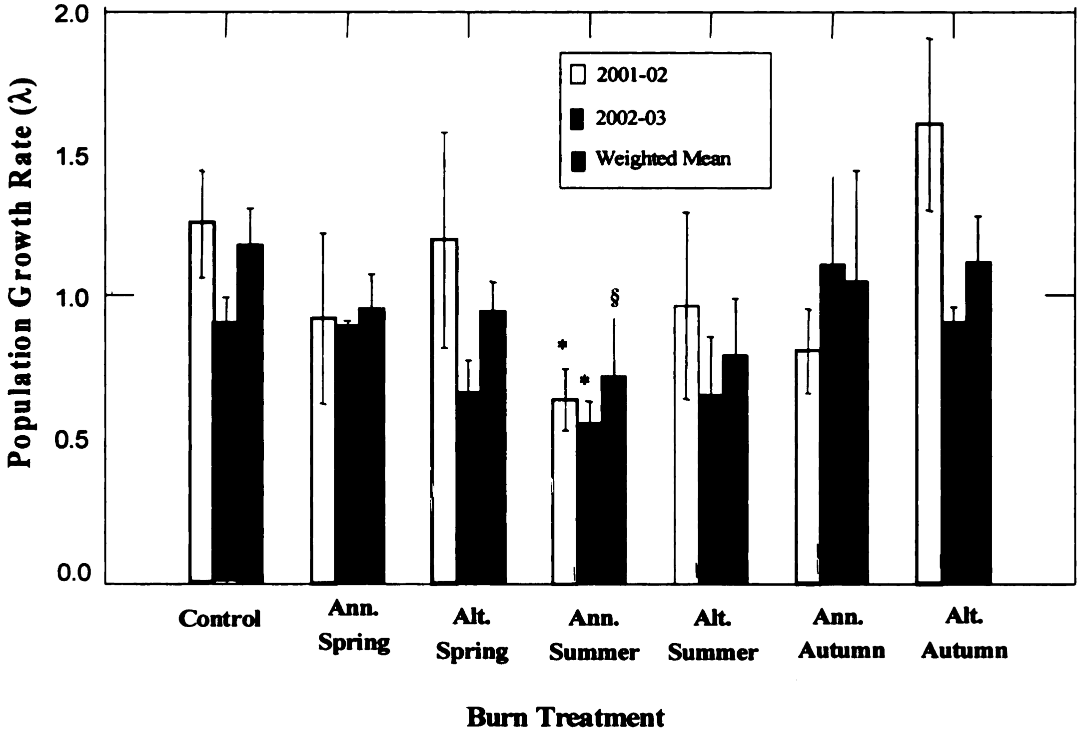


Figure 2.5. Estimated population growth rates of *C. maculosa* in response to season and frequency of burning in southwest Michigan grasslands. Error bars indicate one SE of the mean. Asterisks (*) indicate significant differences when compared to the control (unburned plots) at the *P*=0.05 level; § indicates significance at *P*=0.06.

Life Table Response Experiment analysis

The LTRE analysis further dissects effects of the treatments on population growth rates by examining the contribution of individual matrix transitions on growth rates. This gives insight into the mechanisms by which treatments affect population growth. This analysis showed that changes in individual transitions had variable contributions to overall population growth, though spring and summer treatments consistently had negative impacts on population growth through changes in reproduction (Figure 2.6). Summer burning greatly reduced reproduction (Table 2.1), and the LTRE analysis revealed that this change in reproduction had strong negative effects on population growth, beyond other effects summer burning had on juvenile or adult survival.

Elasticities

In the control populations, non-reproductive adults, juveniles, and reproduction (seedlings) had the highest elasticity values (0.26, 0.23, and 0.23, respectively) indicating that in unmanaged populations, small changes to these life stages would have the greatest effect on overall population growth rates. The burn treatments altered this structure, for example by generally reducing the relative potential importance of reproduction (Table 2.3). In general, non-reproductive adults had high elasticity values across all treatments. Spring burning tended to increase elasticity values for the seedbank, while summer burning increased elasticity values for large adults. Autumn burning did not have any consistent effects on elasticities.

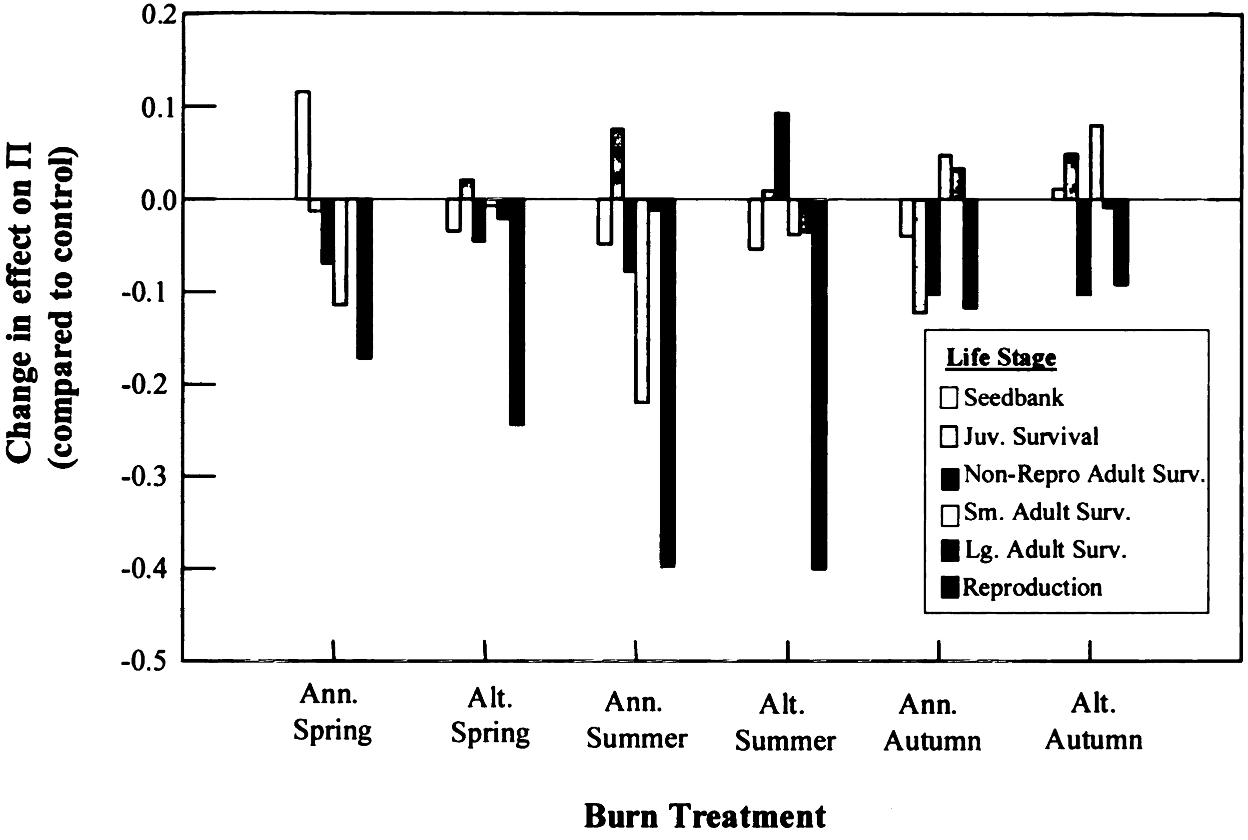


Figure 2.6. Summary of results from the Life Table Response Experiment analysis for effects of burn treatments on life stage transitions. Calculations are based on the weighted average matrix for each treatment across years and sites. Results are expressed relative to performance in control (unburned) treatments.

Table 2.3. Elasticity values for the weighted mean matrix (2001-03) for each treatment.

Treatment	**Seedbank**	**Juvenile**	**Non-repro adult**	**Small adult**	**Large adult**	**Reproduction**
Control	0.036	0.234	0.2567	0.144	0.095	0.234
Ann. Spring	0.219	0.143	0.396	0.047	0.052	0.143
Alt. Spring	0.108	0.203	0.293	0.158	0.116	0.203
Ann. Summer	0.000	0.157	0.203	0.148	0.335	0.157
Alt. Summer	0.135	0.179	0.244	0.044	0.219	0.179
Ann. Autumn	0.000	0.157	0.301	0.063	0.233	0.157
Alt. Autumn	0.194	0.241	0.095	0.146	0.085	0.201

Discussion

This study shows that a transition matrix modelling approach can give valuable insight into effects of a management treatment, like prescribed fire, on invasive species populations. In our experiment, biomass harvests in 2001 and 2002 showed no effect of burning on the relative abundance of *C. maculosa,* whereas the transition matrix analysis revealed a significant decline in population growth from summer burning. Biomass harvests in this study gave an incomplete picture of the actual effects of our management treatments because they mainly reflected effects on the size and abundance of adults (the major constituent of aboveground biomass). Seedling and juvenile dynamics, as well as reproduction, were not detected in biomass responses. By accounting for each life stage, a more accurate understanding of the population dynamics of *C. maculosa* is possible.

Treatment Effects

Annual summer burning was the only management treatment that reduced population growth of *Centaurea maculosa* in this system. The LTRE analysis indicated that summer burning reduced population growth by reducing reproduction. The timing of the summer burn occurs when *C. maculosa* individuals are starting to flower. The low intensity fire kills the flowering stalk, probably by destroying photosynthetic mechanisms and cell membranes (Salisbury & Ross 1992). Most individuals are unable to produce another flowering stem within the growing season, effectively reducing reproduction to almost zero.

Spring burning occurs before most *C. maculosa* adults have bolted for the year, and so does not stop surviving individuals from reproducing. Autumn burning occurs after adults have produced seeds, and appears, if anything, to increase germination success of seeds by reducing litter, although this apparently has no long-term effect on population growth.

Our analysis also revealed that the frequency of burning is an important variable in this system. Populations burned only in alternate years showed no significant reduction in growth rate, probably because of the high reproductive output of *C. maculosa* individuals in the off-burn years (2002). This increase in reproduction could possibly be a compensatory response to the lack of reproduction in the previous year, which allows plants to increase resource allocation for reproduction in the following year (e.g. Ehrlén & Van Groenendael 2001). This potential rebounding effect negates the positive control effects of burning.

Elasticity Analysis

Elasticities are often used in conservation management to make predictions about what life stages are critical to focus on when trying to change population growth rates. Several recent papers, however, have warned that management decisions based solely on elasticity analyses may be ineffective because of restrictions on interpretations of elasticity values, such as the often unrealistic assumption of a proportional change on all transitions (e.g. de Kroon *et al.* 2000). Although it is often difficult to effectively target life stages with high elasticity values, it is still possible to affect population growth through large effects on other life stages. Our study is an example of this: while non-reproductive adults had the highest elasticity values in control populations, prescribed summer burning reduced population growth because of the effect on reproduction, despite having very little effect on non-reproductive adult survival. However, the elasticity analysis does suggest that alternate control methods may be more effective if they target non-reproductive adults as well as reproduction.

It is also worth noting that for some treatments, the seedbank stage had fairly high elasticity values. However, we had no way to directly assess effects of fire on survival of seeds in the seedbank, and so had to assume a constant survival rate across treatments. Fire can sometimes reduce seedbank longevity, especially at high intensities that cause soil heating (e.g. Maret & Wilson 2000; Buckley *et al.* 2004), but fires were of relatively low intensity at our sites, and probably had little, if any, negative effect on seed survival below the soil surface. More intense fires may help reduce seedbank survival in this system, but further work on seedbank dynamics is needed. Immediate management approaches should focus on other life stages.

Management Recommendations

Although this experiment was done in one location in southwestern Michigan, USA, the sites studied included a wide range in productivity, species composition, and *C. maculosa* infestation, and so we expect our results can be generalized to a wide range of sites. Across these sites, our results indicate that annual summer burning is the best method for reducing *C. maculosa* populations in Midwestern USA prairie remnants. However, our experience suggests that this management regime may be difficult to sustain in lower productivity sites that do not have sufficient grass cover or production to carry fires year after year. Stands of *C. maculosa* do not carry fire well, so successful burns depend on the presence of matrix grasses, such as *Schizachryium scoparium.* While we believe that our experimental burns were quite realistic and comparable in intensity to other large prescribed burns in the local vicinity, in even higher productivity areas fire may be more intense and have different effects on seedbank and plant survivorship. However, this is probably not an issue as *C. maculosa* is rarely a problem in high productivity grasslands in North America. Management of *C. maculosa* may be most difficult in low-productivity areas that are highly infested. It is also important to note that our models did not explicitly consider density dependence, and so our recommendations may not hold for very high or very low densities of *C. maculosa*, even if burning was possible. New infestations may grow much more rapidly than well established infestations (e.g. Freckleton et al. 2003), and stronger density dependence may become evident at very high population densities. However, for communities with moderate *C. maculosa* cover, such as found in most Midwestern US grasslands, these management recommendations hold.

It is possible that interactions with other management options, such as biocontrols or herbicides, may prove to be more effective than fire alone (e.g. Buckley *et al.* 2004; Paynter & Flanagan 2004). While two biocontrol agents, *Urophora quadrifasciata* and *Urophora affinis* (Diptera: Tephritidae) have been released to some extent in Michigan (Lang, Richard & Hansen 1997), their abundances are very low and appear to have no direct impacts on reproduction (S. Emery, unpublished data), although there may be an as-yet-unknown interaction with prescribed fire. The elasticity analysis suggests that treatments that target non-reproductive adults, such as spot herbicide or intense spot burning, may be more effective ways to reduce population growth in low productivity sites. Spot burning has been shown to be effective in other management efforts (pers. comm. J. McGowan-Stinski; Tu *et al.* 2001).

Although effective in controlling *C. maculosa*, summer burning may not be the ideal management tool for all grasslands. If *C. maculosa* control is the main goal, then summer burning is preferable. However, the responses of other species in the community should also be considered. Many desirable C4 grasses do best under a spring burning regime (Howe 1995), and we found in related experiments that spring burning also enhanced recruitment of native forb species in this site (Gross & Suding 2002). Other studies have shown, however, that summer burns or varied-season burns can also be effective in enhancing native plant diversity in Midwestern USA prairies (Howe 1994). Other non-native species may also respond in different ways and should be taken into consideration, as reductions in one non-native species can often lead to increases in another as competition is relaxed (e.g. Gillespie & Allen 2004).

Conclusions

Our study used matrix population modelling to examine the effect of season and frequency of prescribed fire on population growth of an invasive plant species. Despite the mentioned shortcomings, our analysis of treatment effects on population growth of *Centaurea maculosa* provides a good evaluation of management options. Matrix transition models have limitations, but can give more insight into whole-population responses than evaluation criteria based only on community-level responses, and are often more accessible to managers than more complicated modelling approaches. Clearly, management decisions about when and how to use prescribed fire to control invasive species need to consider the entire life cycle of target species, as well as potential effects on other management goals such as the recruitment or persistence of desirable native species.

Acknowledgments

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CHAPTER 3

DOMINANT SPECIES IDENTITY, BUT NOT ABUNDANCE, REGULATES INVASIBILITY OF PLANT COMMUNITIES

Abstract

Dominant species are known to exert strong influence over community dynamics, although little work has addressed how they affect invasibility. In this study, we examined how dominant species identity and abundance affected invasibility of plant communities. To quantify invasibility, we added seeds of 19 species into patches of old fields dominated by different species (*Andropogon virginicus*, *Bromus inermis*, *Centaurea maculosa*, or *Solidago canadensis*). We found that, independent of species richness and abiotic variables, patches dominated by *Andropogon* were the least invasible, while *Bromus* and *Centaurea* patches had the highest number of species invading. The abundance of the dominant species was rarely a significant predictor of invasion. Species richness was the only other significant predictor of invasion, and counter to many other experimental studies was usually positively related to invasibility. These results suggest that dominant species identity may be as important as species richness in determining invasibility of grassland communities.

Introduction

Invasibility- in its broadest sense- describes the ease with which new species establish in a community, and so is fundamental to our understanding of community dynamics. However, factors that control a community's invasibility are still not well resolved. Most studies examining factors that influence invasibility have focused on how invasion by non-resident species is influenced by species richness, and have not explicitly examined other components of community structure, such as dominance and composition (e.g., see reviews by Hector et al. 2001, Levine et al. 2004), despite the fact that dominant species are known to exert strong influence over community dynamics and ecosystem function (McNaughton & Wolf 1970, Crawley et al. 1999, Grime 2001, Dangles & Malmqvist 2004). While many of the experiments manipulating community species richness do attribute some of the negative relationships between diversity and invasibility to a "sampling effect" (Huston 1997), where increased experimental species richness increased the likelihood of including a strong competitive dominant in the community (Crawley et al. 1999, Hodgson et al. 2002, Lennon et al. 2003, van Ruijven et al. 2003), there are very few studies directly addressing the role of different competitive dominant species in regulating invasibility.

Wardle (2001) proposed that the relative abundance of a dominant species, not just its presence, should affect invasibility in both experimental and observational studies, but there is some debate over whether communities with high dominance (e.g., large proportion of community biomass or density contributed by a single species) should be more or less invasible than communities with high evenness. High dominance in communities may be due to complete use of a limiting resource by the dominant species (Tilman 1982, Robinson et al. 1995), or may indicate underutilization of other resources and so provide a variety of unused niches for minor species (Wilsey & Polley 2002). Most evidence for the role of dominant species identity or abundance in mediating invasibility comes from experimental studies, and these have reported mixed results. In a few cases, invasion was positively related to community dominance (Wilsey & Polley 2002, Smith et al. 2004), suggesting that invading species can exploit underused resources, or that the dominant can facilitate invasion. In other cases, invasion declined with increased dominance (Robinson et al. 1995, Smith & Knapp 1999, Lindig-Cisneros & Zedler 2002), with evidence suggesting that this was mediated by strong effects of the dominant on productivity, light, or litter. However, these experimental studies usually only focus on the ability of a single species to invade synthetic communities constructed from a pre-determined species pool (e.g. Naeem et al. 2000), or confounded manipulation of community species richness with disturbance caused by species removal (e.g. Smith et al. 2004). Because different processes may influence the assembly of natural and experimental communities (e.g. Ricklefs 2004), there is a need for experiments in natural systems to address the role of dominance in regulating invasion.

In this study, we asked two questions: 1) Does the identity of the dominant species affect invasibility? and 2) Does the relative abundance of the dominant affect invasibility? We compared effects of dominant species with effects of other factors such as community species richness and biomass. We tested these questions in a seed-addition study in two mid-successional old field plant communities in southwest Michigan which were similar in vegetation composition.

Methods

Experimental design

In March of 2004, we established 96 1m x 1m plots across two old fields (64 plots in Site 1 and 32 in Site 2) at Michigan State University's W.K. Kellogg Biological Station (KBS) in SW Michigan (Kalamazoo County; 42° 24' N, 85° 24' W). The two sites had similar soils (Kalamazoo sandy loam) and had been abandoned from agriculture

25 (Site 1) and 40+ (Site 2) years prior to establishment of this experiment. Site 1 had been mowed occasionally following abandonment; Site 2 had been unmanaged.

Both fields had similar assemblages of perennial forbs and grasses, and within each field there were patches dominated by different species. We selected patches dominated by one of four species that were common in both fields - *Andropogon virginicus* L., *Bromus inermis* Leyss., *Centaurea maculosa* Lam., or *Solidago canadensis* L. - and used these patches (hereafter referred to by genus name) for the experimental seed invasion experiment. These four species represented a range in functional types and nativity. *Bromus inermis* is a non-native C3 clonal grass, *Centaurea maculosa* is a non-native forb, *Solidago canadensis* is a native clonal forb, and *Andropogon virginicus* is a native C4 bunch grass. We defined dominance as ≥40% relative cover of the dominant species in the plot based on visual estimates in August using a cardboard square that represented 2% cover for reference. This was an arbitrary, but relatively effective, distinction of patch types within the field. Patches ranged in size from 5-50 m^2, and were separated from other patch types by at least 5m. For each patch type, we haphazardly laid out 1m x 1m plots; 16 in Site 1 and eight in Site 2, as Site 1 was twice as large as Site 2.

We added 50 seeds of 19 different plant species to a 0.25m x 0.5m subsection of each plot in early spring (March) to take advantage of possible freeze/thaw requirements needed for germination. The species added were all common to old-fields and grasslands of SW Michigan (Rabeler 2001) and represented a variety of functional types and nativity (Table 3.1). These species were chosen based on seed availability, seed size (no very

Table 3.1. Species added as seeds to experiments. Origin refers to North American presence.

Species	Life Form	Origin
Achillea millefolium	forb	native
Andropogon gerardii	C4 bunchgrass	native
Bromus inermis	C3 clonal grass	non-native
Bromus kalmii	C3 bunchgrass	native
Calamagrostis canadensis	C3 clonal grass	native
Centaurea maculosa	forb	non-native
Coreopsis lanceolata	forb	native
Dactylis glomerata	C3 bunchgrass	non-native
Desmodium canadensis	legume	native
Echinacea pallida	forb	native
Elymus canadensis	C3 clonal grass	native
Lespedeza capitata	legume	native
Liatris aspera	forb	native
Muhlenbergia racemosa	C4 clonal grass	native
Panicum virgatum	C4 clonal grass	native
Poa pratensis	C3 clonal grass	non-native
Ratibida pinnata	forb	native
Schizachyrium scoparium	C4 bunchgrass	native
Solidago nemoralis	forb	native

large or very small seeds), and plant family (Poaceae, Asteraceae, or Fabaceae only as some control for phylogenetic relationships). In August, we censused the plots to determine which species had established in the seed-added plots, and compared this to establishment from the extant species pool in adjacent subplots to which no seeds had been added. To compare our results with other studies, we used three measures of invasibility: 1) the net total number of seedlings established in the seed-added subplot, 2) the net total number of non-native seedlings established, and 3) total number of species (maximum of 19) established in these plots.

Environmental correlates

To assess whether vegetation patches dominated by different species or located in different sites differed in other variables that might also affect invasibility, we measured light levels below the vegetation (photosynthetically active radiation, PAR), soil moisture, moss cover, available inorganic nitrogen, aboveground plant biomass, and plant community species richness and evenness. We determined PAR in each plot early (May) and late (August) in the growing season using a Sunfleck Ceptometer (Decagon Devices, Inc.) (in Site 2, light levels were only measured in August). Within each plot we took three PAR measures within +/-2 hr of solar noon in full sun (1m above the plots) and at three points at ground level (under the vegetation and litter). We averaged these three measures to obtain an estimate of the percentage of full sunlight penetrating to ground level for each plot.

We measured available soil inorganic nitrogen and soil moisture in each plot in May. Two soil cores (10 cm depth, 1.9 cm diameter) were taken from areas immediately adjacent to the plots. Samples were placed on ice in the field and then processed in the lab within 24 hrs of sampling. Soils were sieved (2mm sieve) to remove vegetation, roots, and rocks, and sub-sampled for gravimetric soil moisture and inorganic nitrogen content within 24 h of sampling. Gravimetric soil moisture was determined by weight loss after drying 10-15 g soil at 105°C for 24 h. For the nitrogen assays, we extracted 20 g fresh soil in 50 ml 1M KCl. These samples were shaken for 1 min, settled for 24 h at room temperature, and filtered through a 1-µm Gelman glass filter. The NO_3^- and NH_4^+ concentrations of the extracts were determined using an Alpkem auto-analyzer (Robertson et al. 1999).

In August, we quantified composition in each plot from visual estimates of relative cover of all plant species, including moss, using a reference square of 2% cover. Species that were below the canopy were recorded as <1% cover. Because of variations in estimates, percent cover data were standardized to add to 100%. Moss cover was estimated separately and was not part of the 100% standardizations. Species richness and evenness of all vascular plant species were calculated from these visual estimates of community composition. Evenness was calculated as $E = 1/DS$ where S is species richness and D is Simpson's dominance (Simpson 1949) where x_s is the abundance of the s^{th} species:

$$D = \sum_{S=1}^{S} (x_s / \Sigma x)^2$$

This metric is independent of species richness and more responsive to changes in dominant than rare species abundance (Smith & Wilson 1996). We estimated aboveground production from harvests of biomass and litter taken from a 0.25m x 0.50m area immediately adjacent to each plot during peak biomass in mid-August. Samples were dried (48h at 65°C) and then weighed.

Data Analyses

Because of differences in site history, we initially examined invasibility (using net total seedlings) as a function of both site and patch type. There was a significant site effect ($F_{1,87}=16.16$, $P<0.001$), as well as a significant effect of dominant species patch type ($F_{3,87}=5.71$, $P=0.001$). The was no significant interaction between site and patch type ($F_{3,87}=1.66$, $P=0.182$). Consequently, we present results for the two sites separately in order to examine dominant species effects and search for generalizations across the two sites. To summarize variation in biotic and abiotic factors across the four different patch types, we used principal components analysis (PCA) with varimax rotation on the variables of aboveground biomass, litter, light transmittance in May and August, moss cover, total available inorganic soil N, and soil moisture, creating orthogonal variables to use in analyses (Legendre & Legendre 1998). Because of known relationships between species diversity and invasibility in other studies (e.g., Planty-Tabacchi et al. 1996, Foster et al. 2002), we kept species richness and evenness as separate variables. To examine effects of dominant species on invasibility in these communities, independent of other factors, we used one-way ANCOVA with patch type as the main effect, each of the three different measures of invasibility as the response variable, and the PC axes scores and diversity measures that significantly differed across patch types as covariates. Count data were log transformed ($\ln(x+1)$) for analyses. Simple linear regression was used to examine the relationship between invasibility and relative abundance of the dominant species for each patch type. All analyses were performed using Systat v.11.

Results

Environmental variability

For Site 1, three principal components (PC) axes explained 65% of the variation in biotic and abiotic factors across the four vegetation patch types. May and August light levels had the highest loadings on PC1. Soil moisture and available inorganic soil N were correlated with PC2, while aboveground biomass loaded highest on PC3 (Table 3.2). Because of these loadings, we loosely defined PC1 as "light" and PC2 as "soil". For Site 2, two PC axes explained 69% of the variation in biotic and abiotic factors. Aboveground biomass, light availability, and available inorganic soil N loaded high on PC1, "productivity," while percent moss and soil moisture had highest loadings on PC2, "moisture" (Table 3.2).

The four vegetation patch types in Site 1 differed significantly in the first two PC axes (Table 3.2). Patches dominated by *Centaurea* had higher light levels (PC1) than the other patch types ($F_{3,53} = 7.42$, $p<0.001$), while soil N was lowest under *Andropogon* patches (PC2) and highest under *Bromus* patches ($F_{3,53} = 11.07$, $P<0.001$). *Bromus* patches also had lower species richness than the other patch types ($F_{3,53} = 5.67$, $P=0.012$). There was no significant differences across patch types in aboveground biomass (PC3: $F_{3,53} = 1.05$, $P=0.381$) or evenness ($F_{3,53} = 1.37$, $P=0.27$). In Site 2, *Andropogon* patches had the lowest "productivity" (PC1) while *Solidago* had the highest "productivity" ($F_{3,32} = 7.56$, $P<0.001$). *Bromus* patches had higher soil moisture (PC2) than the other patch

Table 3.2. Variable weightings for the first two or three principal components used to describe environmental variability across patch types. Variables with highest loadings are in bold. Mean PC scores for each patch type are also included (standard errors in parentheses).

Variable	PC1	PC2	PC3
SITE 1:			
Biomass	0.226	-0.164	**-0.866**
Litter	0.472	-0.047	0.415
%moss cover	0.392	-0.168	0.627
%soil moisture	0.263	**0.814**	0.128
May light levels	**0.732**	0.146	-0.113
Aug. light levels	**0.772**	0.060	0.107
Inorganic soil N	-0.069	**0.891**	-0.099
%Variance Explained	23.33	21.98	19.51
Patch type mean scores:			
Andropogon	-0.07 (0.24)	-0.88 (0.17)	-0.37 (0.35)
Bromus	0.68 (0.19)	0.85 (0.20)	0.10 (0.23)
Centaurea	-1.04 (0.43)	0.08 (0.40)	-0.05 (0.21)
Solidago	0.05 (0.15)	-0.03 (0.18)	0.26 (0.24)
SITE 2:			
Biomass	**0.804**	-0.131	
Litter	0.404	-0.378	
%moss cover	-0.066	**0.837**	
%soil moisture	0.385	**0.810**	
Aug. light levels	**0.893**	0.117	
Inorganic soil N	**0.850**	0.328	
% Variance Explained	41.38	27.31	
Patch type mean scores:			
Andropogon	-0.85 (0.24)	-0.23 (0.40)	
Bromus	0.47 (0.11)	1.13 (0.19)	
Centaurea	-0.43 (0.32)	-0.49 (0.17)	
Solidago	0.76 (0.36)	-0.38 (0.33)	

types ($F_{3,32} = 6.82$, $P<0.001$). *Solidago* patches had the highest species richness, while *Bromus* patches had the lowest species richness ($F_{3,32} = 8.67$, $P<0.001$). As in Site 1, there was no difference in evenness across patch types in Site 2 ($F_{3,32} = 0.942$, $P<0.427$).

Dominant species identity and invasibility

To examine effects of dominant species on invasibility, we used only those variables that significantly differed across vegetation patch types as covariates in the ANCOVA. After accounting for species richness and environmental variables (PC scores), an ANCOVA indicated that there were still marginally significant effects ($p=0.06$) of patch type on invasibility (measured as net total seedlings) in Site 1 (Table 3.3). Patches dominated by *Andropogon* were least invasible in terms of total numbers of seedlings (Figure 3.1a,b), while *Centaurea* patches tended to have highest number of total seedlings invading. There were no significant differences among vegetation patch types in the number of species able to invade or in the total numbers of non-native seedlings that invaded.

In contrast, in Site 2, identity of the dominant species was a significant predictor of all three measures of invasibility, even after accounting for the covariates of species richness and environmental variability (Table 3.3). Patches dominated by *Bromus* were most invasible while, as in Site 1, *Andropogon* patches tended to be least invaded (Figure 3.1a,b).

Table 3.3: Results for ANCOVA using composite environmental variable (PCs) and species richness as covariates to test for the effects of patch type on three measures of invasibility.

Site 1 Final model fit: Total seedlings: R2=0.25; Seedling SR R2=0.18; Non-Native Seedlings:R2=0.22

Site 2 Final model fit: Total seedlings: R2=0.60; Seedling SR R2=0.62; Non-Native Seedlings:R2=0.61.

		Total Seedlings			**Seedling Species Richness**			**Non-Native Seedlings**		
	df	MS	F	P	MS	F	P	MS	F	P
Site 1:										
Patch Type	3	1.453	2.613	**0.063**	2.421	0.553	0.649	1.158	2.057	0.119
PC1-light	1	0.906	1.629	0.208	15.555	3.554	0.066	1.633	2.9	0.095
PC2-soil	1	0.264	0.475	0.494	0.767	0.175	0.677	1.128	2.004	0.164
Species Richness	1	2.173	3.906	**0.054**	8.704	1.989	0.165	2.083	3.7	**0.061**
Error	46	0.556			4.377			0.563		
Site 2:										
Patch Type	3	2.251	5.628	**0.004**	14.897	7.98	**0.001**	2.852	7.051	**0.001**
PC1-productivity	1	0.046	0.116	0.736	2.103	1.127	0.299	0.705	1.744	0.199
PC2-moisture	1	0.2	0.5	0.486	1.189	5.994	**0.022**	0.629	1.554	0.224
Species Richness	1	5.86	14.654	**0.001**	23.972	12.842	**0.001**	2.817	6.962	**0.014**
Error	25	0.4			0.867			0.405		

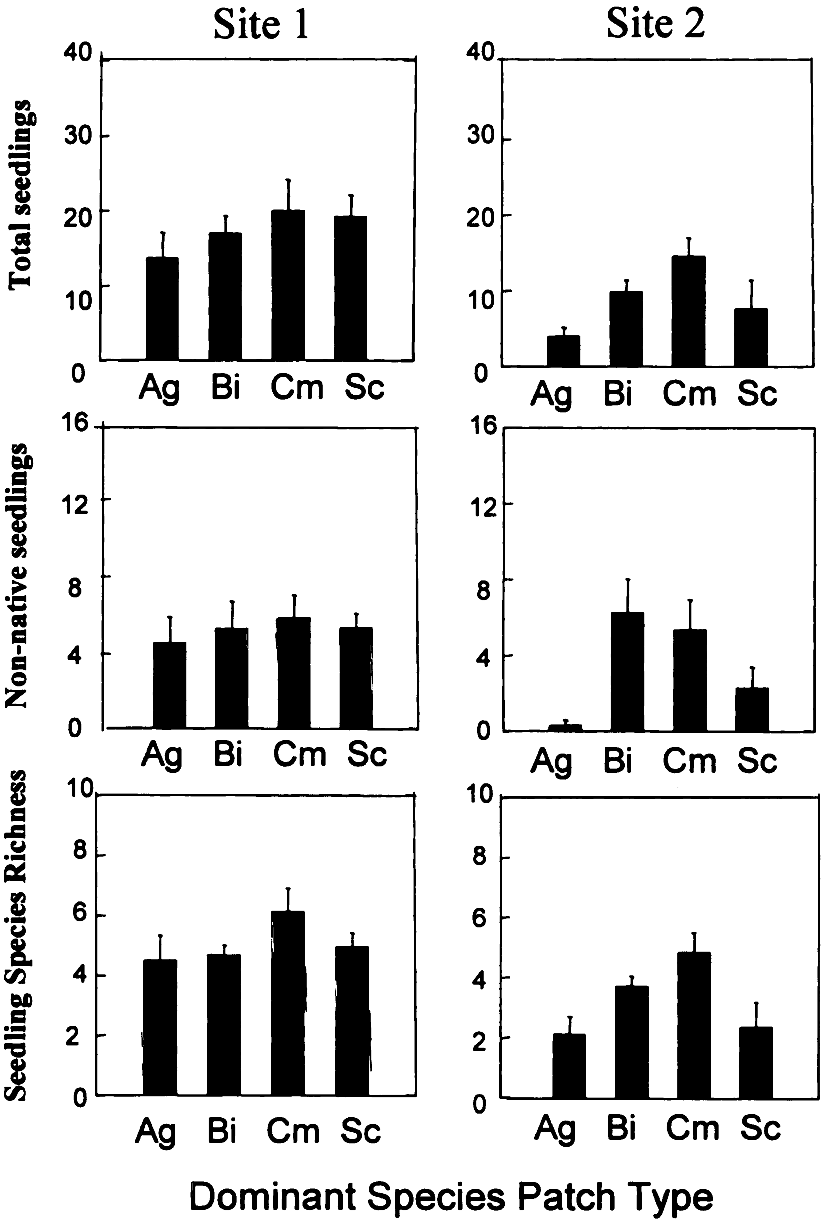

Figure 3.1a. Raw data for comparative invasion success following seed addition (19 species added) into the four different vegetation patch types in two different old fields in SW Michigan, USA. Patch types are abbreviated: *Andropogon virginicus* (Av), *Bromus inermis* (Bi), *Centaurea maculosa* (Cm), *Solidago canadensis* (Sc). Bars represent one standard error.

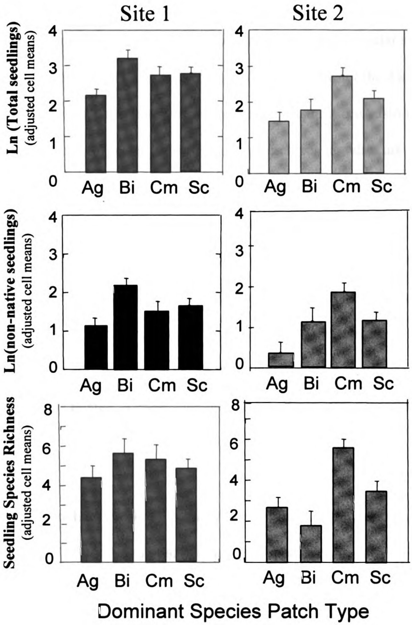

Figure 3.1b. Adjusted cell means from ANCOVA for comparative invasion success following seed addition (19 species added) into the four different vegetation patch types in two different old fields in SW Michigan, USA. Letters indicate significant differences in the ANCOVA at the p<0.05 level, using Tukey multiple comparisons tests. Patch types are abbreviated as in Figure 3.1a.

Dominant species abundance and invasibility

Although all of the patches were dominated by one particular species (defined as ≥40% cover), there was a fairly large range in relative cover of the dominant within each patch type (40-93%). In Site 1, none of the three measures of invasibility varied with cover of the dominant species (only seedling species richness data are shown in Figure 3.2). However, in Site 2, relative cover of the dominant species was related to invasibility for some of the patch types (Figure 3.2). In *Solidago* dominated patches, total number of seedlings (R^2=0.51, P=0.045) and seedling species richness (R^2=0.49, P=0.05) declined with increasing cover of the dominant. For *Bromus* dominated patches, though, cover of the dominant was positively related to the total number of species establishing from added seeds (R^2=0.74, P=0.006). In neither site was cover of the dominant species related to establishment success of non-native species.

Other factors

Species richness within a patch type was often a significant covariate in the ANCOVA (Table 3.3). For all patch types, plot species richness was positively related to invasibility (only seedling species richness shown in Figure 3.3). In no situation was there a negative relationship. Of the abiotic variables measured, soil moisture was positively related to the number of species invading in Site 2, but not Site 1, and May light levels were negatively related to seedling species richness in Site 1, but not Site 2. None of the other variables we measured were related to invasibility.

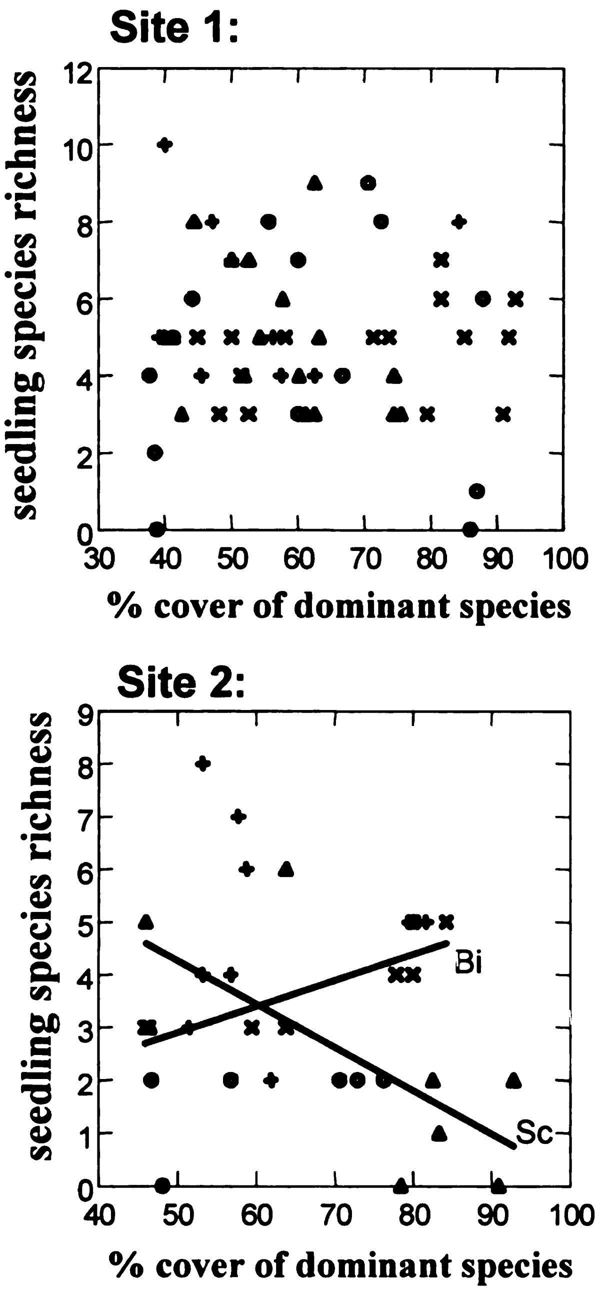

Figure 3.2. Relationships between % cover of the dominant species in each community and seedling species richness. For all figures, circles are *Andropogon* (Av) dominated patches, x-es are *Bromus* (Bi) dominated, crosses are *Centaurea* (Cm) dominated, and triangles are *Solidago* (Sc) dominated. Dominance was defined as >40% cover (see text for details) Regression lines are shown when relationships have a p<0.05.

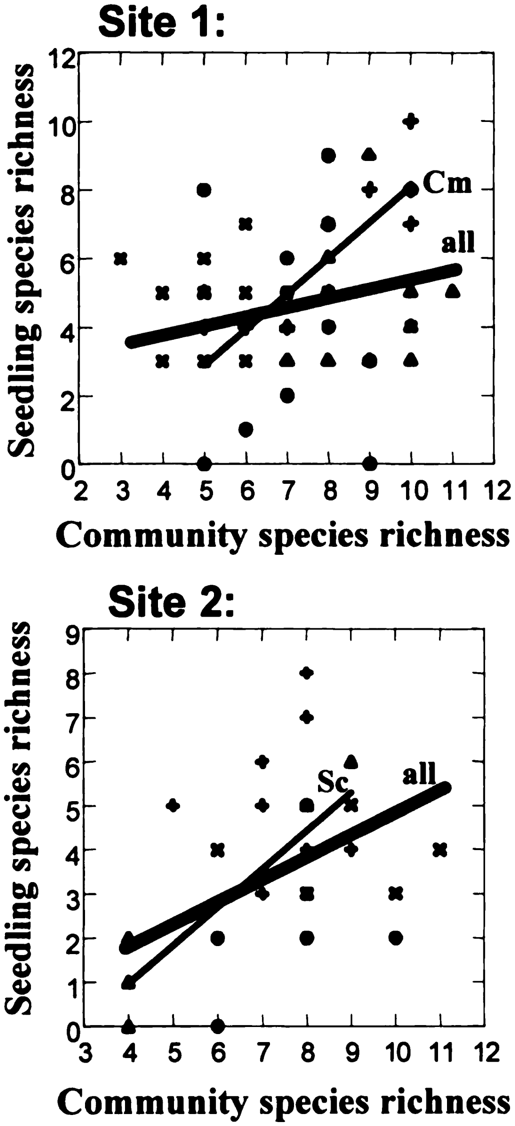

Figure 3.3. Relationships between patch species richness and seedling species richness in sites. Regression analyses are as follows: site 1) all: $R^2=0.07$, $p=0.045$; C: $R^2=0.44$, $p=0.05$; site 2) all: $R^2=0.24$, $p=0.005$; S: $R^2=0.79$, $p=0.003$. All other relationships are non-significant. Symbols are as in Figure 3.2.

Discussion

Dominant Species Effects

In this experiment we found that identity of dominant species affected local invasibility, above and beyond any biotic or abiotic effects that we measured within these vegetation patches. In both sites, *Andropogon*-dominated patches were the least invasible; in Site 1 *Bromus* patches, and in Site 2 *Centaurea* patches tended to be the most highly invaded. Interestingly, these species effects were only detectable once variation in correlated factors (e.g. species richness, productivity, etc.) was accounted for in the analyses. For example, when examining the raw data *Bromus*-dominated patches did not appear to be more highly invasible than other patch types, but once variation in light levels, soil nutrients, and species richness were accounted for, *Bromus* dominated sites were the most invasible patch type in Site 2.

It is possible that factors not measured in this study, particularly those that operate belowground, are driving the differences in invasibility we observed among these vegetation patches. For example, *Andropogon* is known to be a strong competitor for belowground resources, especially in the presence of mycorrhizae (Hartnett et al. 1993); if soil phosphorus levels are greatly reduced in these patches, this may explain why areas dominated by this species in both communities had low invasibility. Other studies have reported that individual species effects on invasion may be due to allelopathy (e.g. Callaway et al. 2004) or feedbacks between plant species and associated soil biota, microbes, or soil invertebrates (Klironomos 2002, vanRuijven et al. 2003). In this study, we were unable to address such species-specific effects, and there is a definite need for further in-depth studies of plant-soil interactions.

It is also possible that other species that consistently co-occur with the dominant species in these communities are driving the species-correlated differences in invasibility that we observed in this study. For example, Lindig-Cisneros & Zedler (2002) found that it was the abundance of particular subordinate species that reduced invasion by reed canary grass more than the identity of the dominant species in fen habitats. Other studies have reported that rare species are important in reducing invasibility of plant communities (Zavaleta & Hulvey 2004, Lyons & Schwartz 2001). While both sites in our study share a common regional species pool, there were detectable differences in species composition among the four patch types. For example, across both sites two C3 grasses, *Danthonia spicata* and *Phleum pratense,* only occurred in *Andropogon*-dominated patches, whereas *Stellaria media* and *Chrysanthemum leucanthemum*, both dicots, occurred more often in *Solidago*-dominated plots. However, no particular subordinate species was consistently detected in all plots within a patch type so it is unlikely that these subordinate species were important in controlling the invasibility of plots that varied in dominant species composition.

Relative Abundance of Dominants

Interestingly, although we detected significant effects of dominant species type on invasibility, the relative abundance of these species in a patch did not generally affect invasibility. In Site 2, there was some evidence for species abundance affecting invasibility, but there were no consistent patterns across patch types. In *Bromus*-dominated patches, invasibility increased with relative *Bromus* cover. In contrast, for *Solidago* patches, invasion was reduced in plots with high dominance. The lack of a relationship between species abundance and invasibility in this study is surprising, given results from other experimental studies that find that dominance (relative abundance of the dominant species) to be an important predictor of invasion (e.g. Robinson et al. 1995, Prieur-Reichard et al. 2002, Smith et al. 2004). Also, some recent theory predicts that community evenness has an important role in ecosystem functioning (Nijs & Roy 2000) and so would be expected to influence invasion. Our results do not necessarily negate the importance of abundance, but do suggest that beyond a certain threshold (e.g. 40% cover), relative cover aboveground of the dominant species may have little effect on community functioning. It is possible that the plot size we used in this study was small enough so that belowground interactions with the dominant species were similar regardless of whether they had 40% or 90% cover. Belowground competitive neighborhoods may be much larger than above-ground neighborhoods (Hawkes & Casper 2002), and at least one study has shown that belowground competition may be independent of aboveground diversity (Cahill 2003).

Species Richness

In contrast to results from many other experimental studies, we found that local species richness was often positively related to invasibility in these communities (Table 3.2). Because our study plots were similar in size to small-scale experimental studies and environmental variability between plots within a patch type was minimal, we expected that species rich plots within a patch type would be less invasible due to competitive interactions (niche complementarity, e.g., Tilman 1997), whereas across species patch types species rich plots would tend to be more invaded due to underlying abiotic gradients favoring high diversity (e.g, Stohlgren et al. 1999, Knight & Reich 2005). These different relationships are predicted because of differences in driving factors at different scales of study (Levine & D'Antonio 1999, Shea & Chesson 2002, Byers & Noonberg 2003). Most studies that have reported positive relationships between community species richness and invasion (or abundance of non-native species) have focused on large spatial scales; few studies have reported a positive relationship at small spatial scales (e.g. Knight & Reich 2005, though see Robinson et al. 1995, Stohlgren et al. 1999), which has reinforced the hypothesis that environmental variability drives the relationship between diversity and invasion. However, at the small scale of our study we found only positive relationships between diversity and invasion, suggesting that other mechanisms besides landscape-level environmental variability can create positive diversity-invasibility relationships, and that the negative diversity-invasibility relationships found in manipulative experiments may not accurately reflect natural systems. Since environmental variability within patch types was minimal in our study, some other mechanism must be operating. It may be that the 'diversity begets diversity' hypothesis that is commonly invoked to explain positive relationships at larger spatial scales (e.g. Stohlgren et al. 1999) may also operate at smaller spatial scales. For example, Palmer & Maurer (1997) have proposed that a high diversity of interacting subordinate species may create increased micro-heterogeneity, allowing even more species to invade. More work examining other possible mechanisms is needed, though.

Conclusion

Understanding all factors influencing dynamics of invasion is essential for habitat protection and restoration. Our work has shown that identity of dominant species may be as important as species richness in regulating community invasibility as measured by seedling recruitment into communities. While this was only a year-long study in a perennial grassland, several studies of invasive species and of plants in general have shown that seedling recruitment is a key life stage in population growth (e.g. Silvertown et al. 1993, Shea and Kelly 1998, Parker 2000). This knowledge may help managers and practitioners select effective species to use as dominants in restoration efforts to reduce or limit further invasions, or to use in native species seed additions to take advantage of highly invasible non-native communities (e.g., Seabloom et al. 2003, Suding et al. 2004). For example, both *Bromus* and *Centaurea* are non-native species and had high invasibility in our study, suggesting that reverse "invasions" of native species into these communities may be a viable approach in restoration efforts, though such high invasibility may also be a mechanism whereby positive feedbacks reinforce exotic invasions. While ecologists continue to search for generalities, it is important to remember that species identity, as well as diversity, can play a large role in community dynamics.

Acknowledgments

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CHAPTER 4

RELATIONSHIPS BETWEEN COMMUNITY EVENNESS, DOMINANT SPECIES IDENTITY, AND INVASION IN EXPERIMENTAL PLANT COMMUNITIES

Abstract

While there has been extensive interest in understanding the relationship between diversity and invasibility of communities, most studies have only focused on one component of diversity: species richness. However, recently there has been a call to better understand how other components of diversity, such as species identity or community evenness, might affect invasibility. Field studies that measure invasibility may be confounded by variation in soil or other site conditions that co-vary with changes in to these factors. We designed a mesocosm experiment which controlled for soil heterogeneity and species richness while varying dominant species identity and abundance to explicitly test whether: 1) communities with high evenness are more resistant to invasion, and 2) identity of dominant species in communities can affect invasibility. We found that the identity of dominant species significantly affected establishment of invaders, but that evenness of communities was rarely important in predicting invasion. Using structural equation modeling, we found light interception and community biomass to be key mechanisms that determined invasion success of seedlings. Nitrogen availability was important in determining survival of invaders through the second year of the experiment. Further, we found significant direct effects of dominant species, especially *Coreopsis lanceolata*, on invasion. Our analyses were not able to identify the additional mechanisms that determined how or why the sites dominated by this species have low invasibility. The effect sizes of dominant species on invasibility in this study are equal to or greater than effect sizes measured in studies examining

relationships between species richness and invasion, suggesting that species composition plays an important role in regulating invasion in communities.

Introduction

Understanding the function and maintenance of biodiversity in communities has been a driving direction of ecological research (e.g., Tilman 1999 and references therein). However, much of the theory and experiments developed about the role of biological diversity for ecosystem functioning has focused solely on aspects of species richness in communities (Tilman et al. 1997, Lehman and Tilman 2000, Loreau et al. 2001). For example, in many experimental studies, communities with high species richness tend to more fully utilize resources, have higher productivity, have lower invasibility, and are more stable than those with lower species richness (e.g., Tilman 1996, Knops et al. 1999, Levine 2000). Though diversity is composed of more than just species richness, very little theory or empirical work has addressed the importance of other aspects of biodiversity for community functioning.

Recently, there has been a call to acknowledge and better understand the role of other aspects of biodiversity, such as species evenness and species composition/identity in community structure and function (Callaway et al. 2003, Wilsey et al. 2005, O'Connor and Crowe 2005). Recent theoretical and experimental studies have examined relationships between evenness and ecosystem functioning, and have found that communities with high evenness should more fully utilize resources than communities with high dominance. For example, Nijs and Roy (2000), show that community evenness is predicted to be positively related to community nutrient uptake and biomass. They raise the caveat, though, that reducing the abundance of strongly competitive species (thus increasing evenness) may result in a decrease in ecosystem function. This points to the importance of species composition. For example, the relationship between community evenness and biomass varied depending on species composition in a diversity manipulation experiment in Europe (Mulder et al. 2004). Plots with large dominant species (those with high biomass in monocultures) showed no relationship between biomass and evenness, while plots with smaller dominant species (those with lower biomass in monocultures) showed negative relationships between biomass and evenness.

While the number of experiments examining relationships between community evenness, species identity, and other community traits such as productivity are growing, understanding how these community traits can interact to influence invasibility is relatively unexplored. Many experimental studies have found evidence for a negative relationship between species richness and invasibility (see reviews in Levine and D'Antonio 1999, Hector et al. 2001). Only two studies have explicitly examined the relationship between evenness and invasibility. In one study, Wilsey and Polley (2002) manipulated the evenness of four plant species in a field experiment and found that invasion by dicots from natural sources was lower in plots with high evenness. Similarly, Tracy and Sanderson (2004) found that weed density decreased in forage plots planted with an even mixture of forage species. They also found weed abundance varied depending on the identity of the base (most common) species. Plots planted with *Festuca aundinacea* had lower weed invasion than plots with *Bromus inermis*, independent of other aspects of diversity. Several other recent studies have also found significant effects of species identity on invasibility of communities (e.g., Crawley et al. 1999, van Ruijven et al. 2003). For example, in a previous field study, we found significant differences in invasibility among vegetation patches dominated by different species within an oldfield that were independent of differences in species richness and resource availability among patches (see chapter 3 for details).

Several of the studies mentioned above quantified invasibility based on invasion from the extant regional species pool (e.g., Wilsey and Polley 2002, van Ruijven et al. 2003). Studies that only examine natural invasion can be complicated by variability in regional species pools, which can regulate invasion independent of local community characteristics (Houseman 2004, Foster 2001). Such studies have little power to generalize about susceptibility of communities to invasion by novel or introduced species. Seed addition experiments (e.g. Symstad 2000, Foster et al. 2002) can better characterize the invasibility of a community. Further, many studies of invasibility and evenness manipulate natural communities (e.g. Smith et al. 2004) or establish communities directly in the field (e.g., Wilsey and Polley 2002), confounding results with effects of disturbance, microheterogeneity in soil resources, or historical site effects. In this study, we asked whether high evenness communities are more resistant to invasion, and whether dominant species identity, beyond other components of diversity, could alter invasibility of a community. We also examined relationships between community composition, resource availability, and invasibility to determine potential mechanisms whereby community composition could affect invasion. We tested these questions in a controlled experiment using constructed grassland communities in pot ‘mesocosms’ with similar initial soil conditions, and with equal species richness, but manipulated evenness.

We added seeds of 19 different species (both native and exotic) to these communities to quantify invasibility.

Methods

Experimental design

We conducted an outdoor mesocosm experiment at the W.K. Kellogg Biological Station (KBS) in SW Michigan, USA (Kalamazoo County; 42° 24' N, 85° 24' W) to examine whether the identity and relative abundance of different dominant species, independent of community species richness, could affect invasibility. The mesocosms were 0.055 m^3 pots (42cm diameter x 40cm deep) buried in the ground in July of 2003, with the rim of the pots flush with the ground surface. The pots were laid out in a 21 by 5 grid, with 0.5m walkways separating each pot on all sides. Each pot was filled with a 3:2 mixture of local field soil and sand with a 2cm layer of gravel at the bottom of each pot to help with drainage. The pots were filled in July 2003, allowed to settle, and seedlings transplanted to establish the treatments in September 2003.

We established 13 unique mesocosm communities using plugs of eight species common to Midwest US grasslands and known to be dominants in some areas within the region (Table 4.1). The 13 treatments varied in evenness and identity of the dominant, but not in species richness (8 per pot) or number of individuals (48 per pot). Two levels of dominance: HIGH (34:2:2:2:2:2:2:2 planting ratio) and MEDIUM (20:4:4:4:4:4:4:4), and an EVEN treatment were created (6:6:6:6:6:6:6:6) with six of the eight species used as

Table 4.1. Species added as seeds to experiments. Origin refers to North American presence. Species in bold are the eight species transplanted to create initial communities.

Species	Life Form	Origin
Achillea millefolium	forb	native
Andropogon gerardii	C4 bunchgrass	native
Bromus inermis	**C3 clonal grass**	**non-native**
Bromus kalmii	C3 bunchgrass	native
Calamagrostis canadensis	C3 clonal grass	native
Centaurea maculosa	forb	non-native
Coreopsis lanceolata	**forb**	**native**
Dactylis glomerata	C3 bunchgrass	non-native
Desmodium canadensis	**legume**	**native**
Echinacea pallida	forb	native
Elymus canadensis	**C3 clonal grass**	**native**
Lespedeza capitata	**legume**	**native**
Liatris aspera	forb	native
Muhlenbergia racemosa	C4 clonal grass	native
Panicum virgatum	**C4 clonal grass**	**native**
Poa pratensis	C3 clonal grass	non-native
Ratibida pinnata	forb	native
Schizachyrium scoparium	**C4 bunchgrass**	**native**
Solidago nemoralis	**forb**	**native**

dominants (all but *Desmodium* and *Lespedeza*). Planting arrangements were randomized within each pot. Each treatment was replicated eight times (104 pots total). All plugs were grown from seed in the greenhouse during June 2003, and transferred outside under shadecloth and regularly watered in July and August. After transplanting, pots were regularly watered for two weeks to help establishment, and then left alone through the fall and winter. In early May 2004, we weeded the pots to remove species that had emerged from the seedbank or from dispersal into the pots. Individuals were removed from pots by clipping stems with small scissors just below the soil surface to minimize soil disturbance.

Measures of invasibility and resources

To quantify invasibility, we added 50 seeds of 19 different species to each pot in March 2004 (to take advantage of possible freeze/thaw requirements needed for germination.) The species added are all common to old-fields and grasslands of Michigan (Rabeler 2001) and represent a variety of functional types and nativity (Table 4.1). In August of 2004 and 2005, we censused numbers of established individuals of the 19 species we added as seeds. Percent survival of seedlings censused in 2004 was calculated from the 2005 census.

To assess whether vegetation treatments affected resource availability, we measured light levels below the vegetation (photosynthetically active radiation, PAR), soil moisture, and available inorganic nitrogen in May and August 2004, the first growing season. We measured PAR in each pot early using a Sunfleck Ceptometer (Decagon Devices, Inc.). For each pot we took three PAR measures within +/-2 hr of solar noon in full sun (1m above the plots) and at six points at ground level (under the vegetation and litter). We averaged these measures to obtain an estimate of the percentage of full sunlight penetrating to ground level. We also measured available soil inorganic nitrogen and soil moisture in each pot. Two soil cores (10 cm depth, 1.9 cm diameter) were taken from each pot, taking care to avoid any seedlings. Samples were placed on ice in the field and then processed in the lab within 24 hrs of sampling. Soils were sieved (2mm sieve) to remove vegetation, roots, and rocks, and sub-sampled for gravimetric soil moisture and inorganic nitrogen content within 24 h of sampling. For the nitrogen assays, we extracted 20 g fresh soil in 50 ml 1M KCl. These samples were shaken for 1 min, settled for 24 h at room temperature, and filtered through a 1-µm Gelman glass filter. The NO_3^- and NH_4^+ concentrations of the extracts were determined using an Alpkem auto-analyzer (Robertson et al. 1999). Gravimetric soil moisture was determined by weight loss after drying 10-15 g soil at 105°C for 24 h.

We determined the actual community composition and structure in these mesocosms by harvesting senesced biomass in November 2004, when we expected to have minimal impacts on plant survival. Samples were sorted by species, dried (48h at 65°C), and weighed. This biomass was then returned to the pots. In late August 2005, we again harvested live biomass from the pots to determine if there had been further changes in community structure and to get an estimate of aboveground net primary productivity. We also measured belowground biomass by taking two vertical slices (totaling 1/8 of total pot volume) from 28 pots (four replicates each of the HIGH and EVEN treatments) in September 2005. Roots were washed over a screen using a hose, then dried (48h at 65°C) and weighed.

Data analysis

We examined differences in invasibility (total number of seedlings, seedling species richness, and second-year seedling survival) among treatments dominated by different species with one-way Analysis of Variance (ANOVA), comparing only the HIGH dominance and EVEN treatments. We also examined differences in resources (light, nitrogen, soil moisture) and biomass among these treatments with one-way ANOVA. Survival data were arcsine-square root transformed for analyses to improve normality, other data were approximately normal.

We used linear regression to examine the effects of community evenness on invasion. Evenness was calculated as $E_{1/DS}$ (Smith and Wilson 1996), which is a metric that is independent of species richness and more responsive to changes in dominant species abundance than rare species abundance. Initial community evenness was determined based on the planting ratios and the average biomass of individual plants of each species (estimated from 10 plug individuals from each species, dried and weighed, data not shown), so that all 'high' dominance treatments did not have the same $E_{1/DS}$ values because of initial differences in plug biomass. Actual evenness was calculated based on the biomass harvest in August 2004. All ANOVA and regressions were performed in SYSTAT v. 11 (SYSTAT Software, Inc. 2004).

To more explicitly examine mechanisms by which dominant species identity and abundance altered invasibility, we used path analysis (or more generally, structural equation modeling, SEM; see Pugesek et al. 2003, Malaeb et al. 2000 for details) to model the relationships between the relative abundance of each dominant species, resource levels, and invasion. Based on a review of the literature, we expected that light, nitrogen availability, soil moisture, and biomass would all be important predictors of seedling establishment success (e.g. Tilman 1993, Foster and Gross 1998, Prieur-Richard et al. 2002, Garcia-Serrano et al. 2004) and so we focused on these variables in the SEM. We expected community composition (identity and relative abundance of the species used to construct the communities) to affect the availability of these resources. We also included direct effects of the resident species on invasibility to cover unknown factors we did not measure. With these expectations, we constructed an initial model of the relationships between community composition, resources, and invasibility (Figure 4.4). We used the program AMOS (Arbuckle 2003) to evaluate the model's ability to predict each of our three measures of invasibility (number of seedlings, seedling species richness, and second-year seedling survival).

Finally, we used multi-response permutation procedures (MRPP) to examine differences in the composition of invaders among the high-dominance treatments (Zimmerman et al. 1985). MRPP is similar to Multivariate Analysis of Variance (MANOVA) but does not depend on assumptions of normality, which is rare in community count data such as this (McCune et al. 2002). We also used non-metric multidimensional scaling (NMS) to plot the composition of invaders of each mesocosm in ordination space, excluding one outlier pot that had extremely low invasibility. NMS is an iterative, non-eigenvector ordination technique that is ideal to use with species composition data (see Legendre and Legendre 1998, p. 444, and McCune et al. 2002, p. 125 for further details). We used PC-ORD (McCune and Mefford 1999) in the 'slow and thorough' autopilot mode using Bray-Curtis distances for the ordination. Forty runs of the ordination (at random starting configurations and with a maximum of 400 iterations per run) were performed using an instability criterion of 0.00001. These runs were compared to 50 randomized runs in a Monte-Carlo simulation to test the significance of the ordination. This procedure reduced the dimensionality of invader composition, allowing us to summarize differences in composition of invaders based on axis-scores for each pot. We then used the axes scores as measures of 'invader composition' in a SEM, similar to the models described above (see Grace 2003 for an example of this).

Results

Effects of dominant species identity on community invasibility and resources

We found that several measures of invisibility varied with the composition of the pots. The total number of seedlings establishing in 2004, the number of species establishing in 2004, and the second-year survival of seedlings in 2005, all differed across treatments (total seedlings: $F_{6,56}=2.59$, $p=0.029$; seedling species richness: $F_{6,56}=5.21$, $p<0.001$; seedling survival: $F_{6,56}=5.63$, $p<0.001$). Pots dominated by *Coreopsis* and *Schizachrium* tended to have fewer total seedlings and fewer seedling species establishing compared to pots dominated by *Panicum* or *Solidago* (Figure 4.1a,b). *Coreopsis* and *Schizachrium* pots, as well as the EVEN pots, had the lowest second-year survival of seedlings, while *Bromus* pots had the highest percent survival of seedlings (Figure 4.1c).

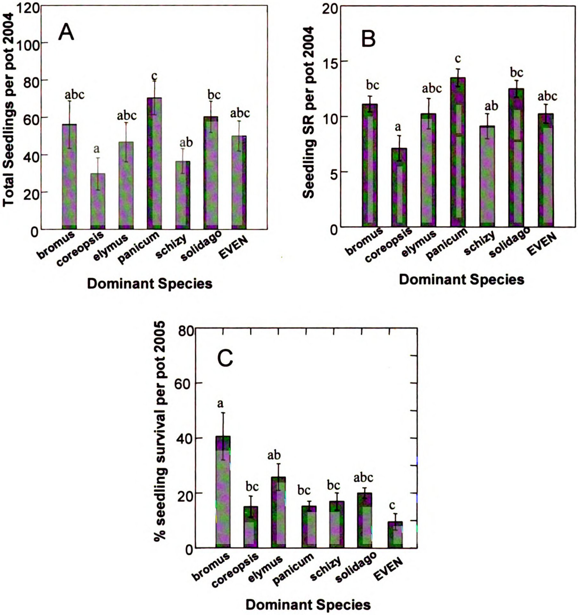


Figure 4.1. Differences in invasibility of treatments with different dominant species. Letters signify differences between treatments (Tukey multiple comparisons test, $p<0.05$).

We also found significant differences among treatments in resource availability and biomass. Available inorganic nitrogen was generally lowest in *Coreopsis*-dominated pots and highest in *Elymus*-dominated pots (May 2004: $F_{6,56}$=5.43, p<0.001; September 2004: $F_{6,56}$=3.07, p=0.012; Figure 4.2a). There were no differences in soil moisture among treatments (May: $F_{6,56}$=0.931, p=0.48; September: $F_{6,56}$=0.41, p=0.87; Figure 4.2b). Light levels below the vegetation differed among treatments in May ($F_{6,56}$=4.98, p<.001), but not in September ($F_{6,56}$=1.29, p=0.28; Figure 4.2c). Plots dominated by *Panicum* and *Solidago* had more light passing through the canopy (less intercepted) in May than the other treatments. *Solidago* pots, and to a lesser extent, *Coreopsis* and *Elymus* pots, had more aboveground biomass in 2004 than the other treatments ($F_{6,56}$=6.14, p<0.001; Figure 4.2d). In 2005, *Coreopsis* pots had significantly more aboveground biomass than all the other treatments ($F_{6,56}$=5.96, p<0.001). Despite these differences in above-ground biomass, belowground root biomass did not differ among treatments ($F_{6,28}$=0.81, p=0.58).

Effects of evenness on invasibility

There were no apparent effects of planted evenness on invasibility (measured as total invader seedling numbers; p=0.79; Figure 4.3a). However, when we examined these patterns using actual evenness based on the 2004 harvest, there was a slight trend for high-dominance pots to have more seedlings than the even pots (R^2=0.05, p=0.022). When we examined relationships between actual evenness and invasibility within each dominant-species treatment, we only found significant relationships for two species, *Elymus* (R^2=0.15, p=0.02) and *Panicum* (R^2=0.38, p=0.01), and these two relationships

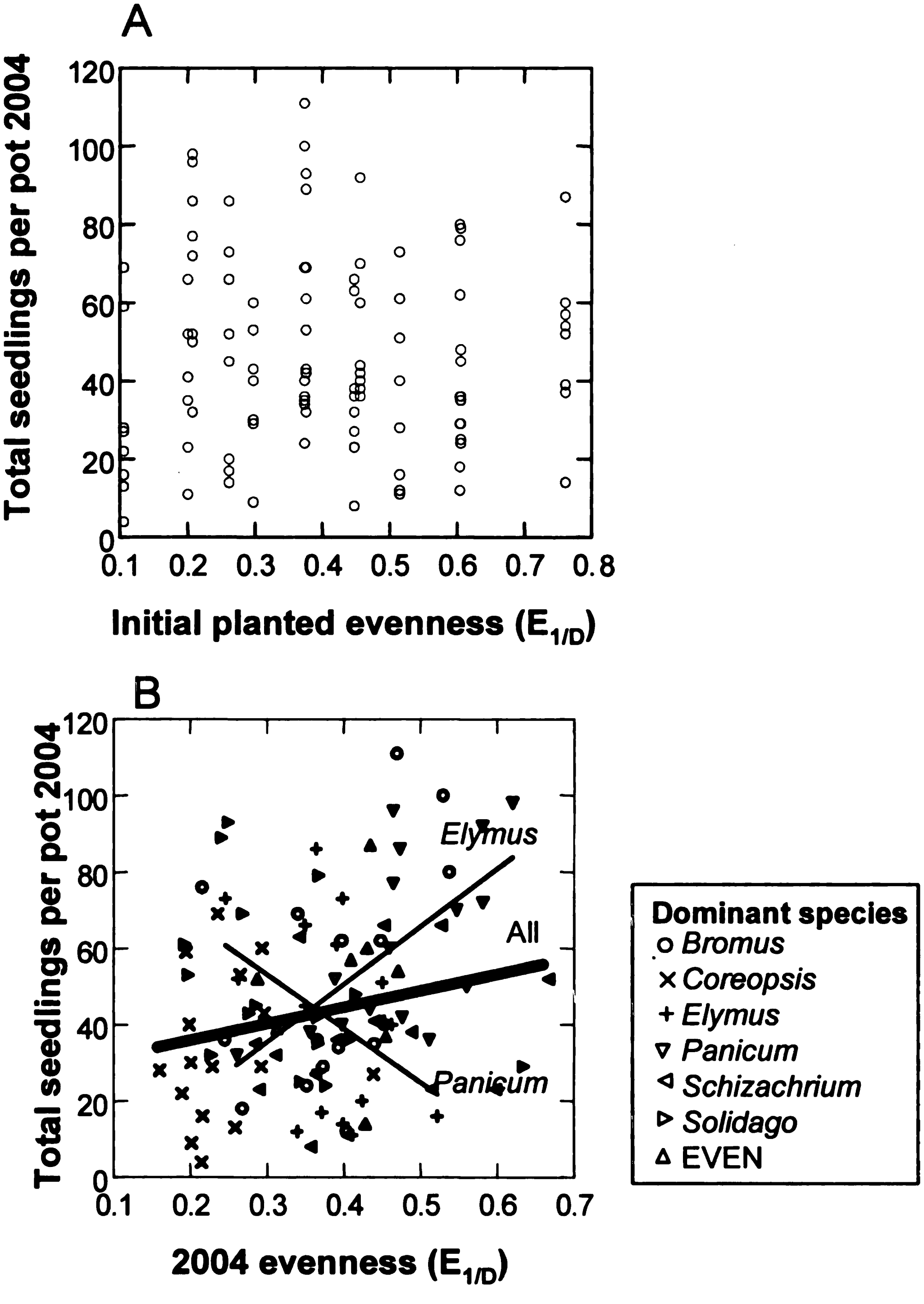


Figure 4.2. Invasibility (# seedlings) as a function of A) initial treatment evenness as planted in 2003; B) actual pot evenness in 2004. In (B), pot identity is shown, where *Elymus* r^2=.15, *Panicum* r^2=.38, All: r^2=.05 (p=0.022). All others are not significant.

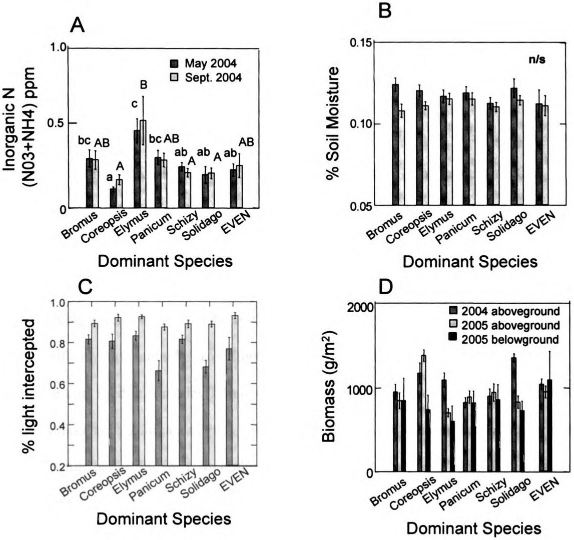


Figure 4.3. Differences in resource availability and biomass among treatments with different dominant species. Letters signify differences between treatments (Tukey multiple comparisons test, $p<0.05$).

were actually in opposite directions (Figure 4.3b). Invasibility was positively related to evenness in *Elymus* pots, but negatively related to evenness in *Panicum* pots.

Mechanisms of invasion

The fit of our initial path analysis model (Figure 4.4) to these data was adequate (goodness of fit index GFI=0.981, where GFI>0.9 indicates a good model fit). Our model described 49% of the variation in invader seedling numbers (Figure 4.5a) and showed that the relative abundance of three species: *Coreopsis*, *Elymus*, and *Schizachrium* had significant direct or indirect effects on seedling numbers (Table 4.2). For seedling species richness, 48% of the variation was explained by the model; indirect effects of *Coreopsis* abundance on invasion were significant, along with the variables from the total seedlings model (Figure 4.5b). Both models showed that light interception and biomass had significant negative effects on invasion, while nitrogen availability and soil moisture had little effect. In both models, *Coreopsis* abundance had a direct negative effect on invasion, beyond the effects that could be attributed to effects on light and biomass. The model also explained 32% of the variation in seedling survival (Figure 4.5c), and two species had significant direct effects: *Elymus* and *Panicum*. Nitrogen availability, as well as light and biomass, were significant predictors of seedling survival. Nitrogen availability was positively related to seedling survival, while biomass and light interception were

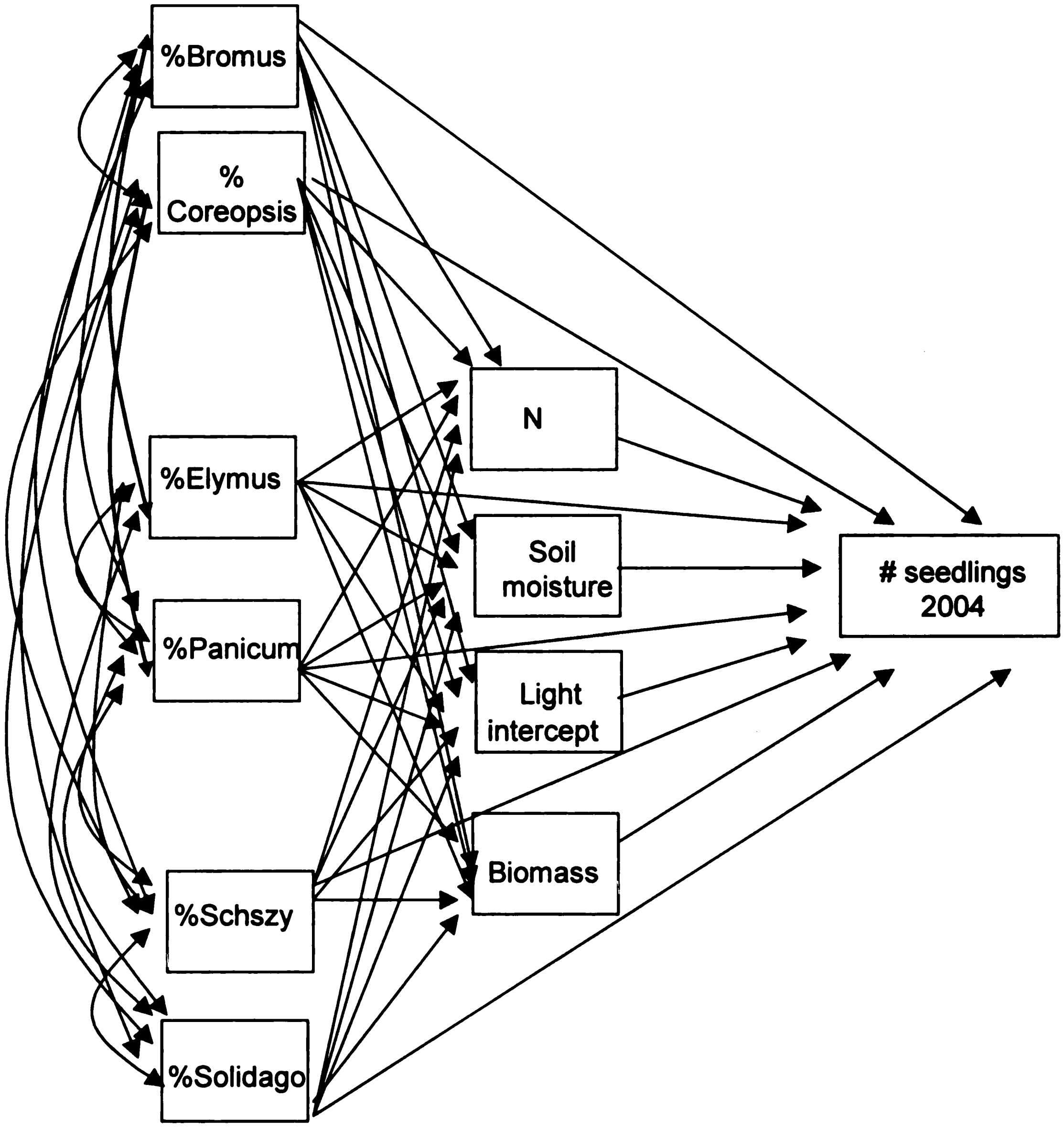


Figure 4.4. Initial structural equation model showing hypothetical relationships between community composition, resources, and invasion. Double-arrows represent correlations among error terms of variables.

A)

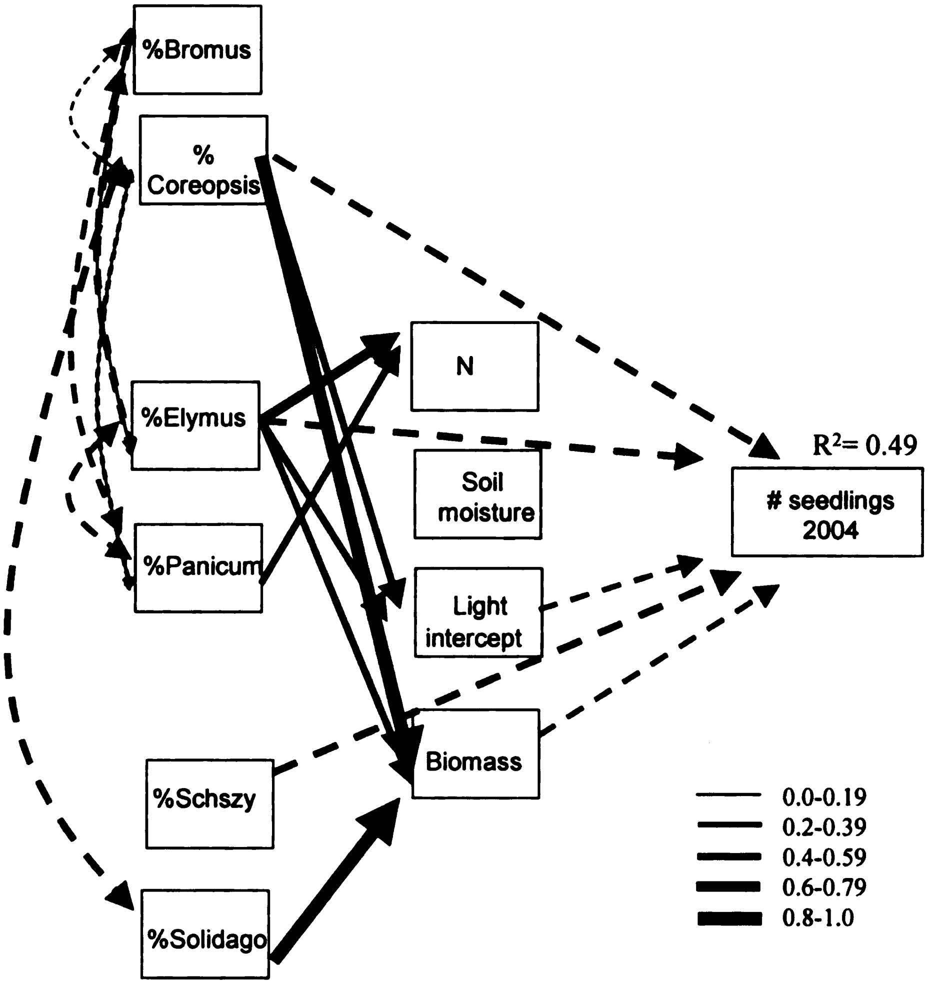


Figure 4.5a. SEM model for predicting total number of seedling invaders in 2004. Non-significant paths are not shown. Line thickness represents standardized regression weights. Positive relationships are shown with solid lines; negative relationships are in dashed lines.

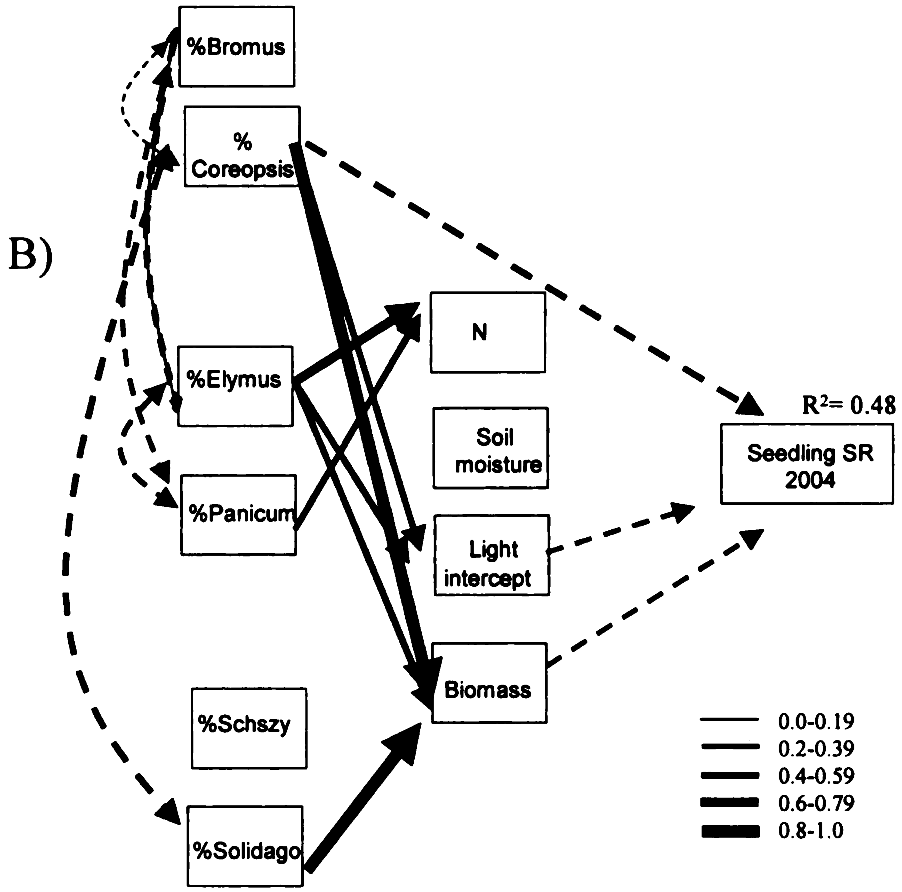


Figure 4.5b. SEM model for predicting species richness of seedling invaders in 2004. Non-significant paths are not shown. Line thickness represents standardized regression weights. Positive relationships are shown with solid lines; negative relationships are in dashed lines.

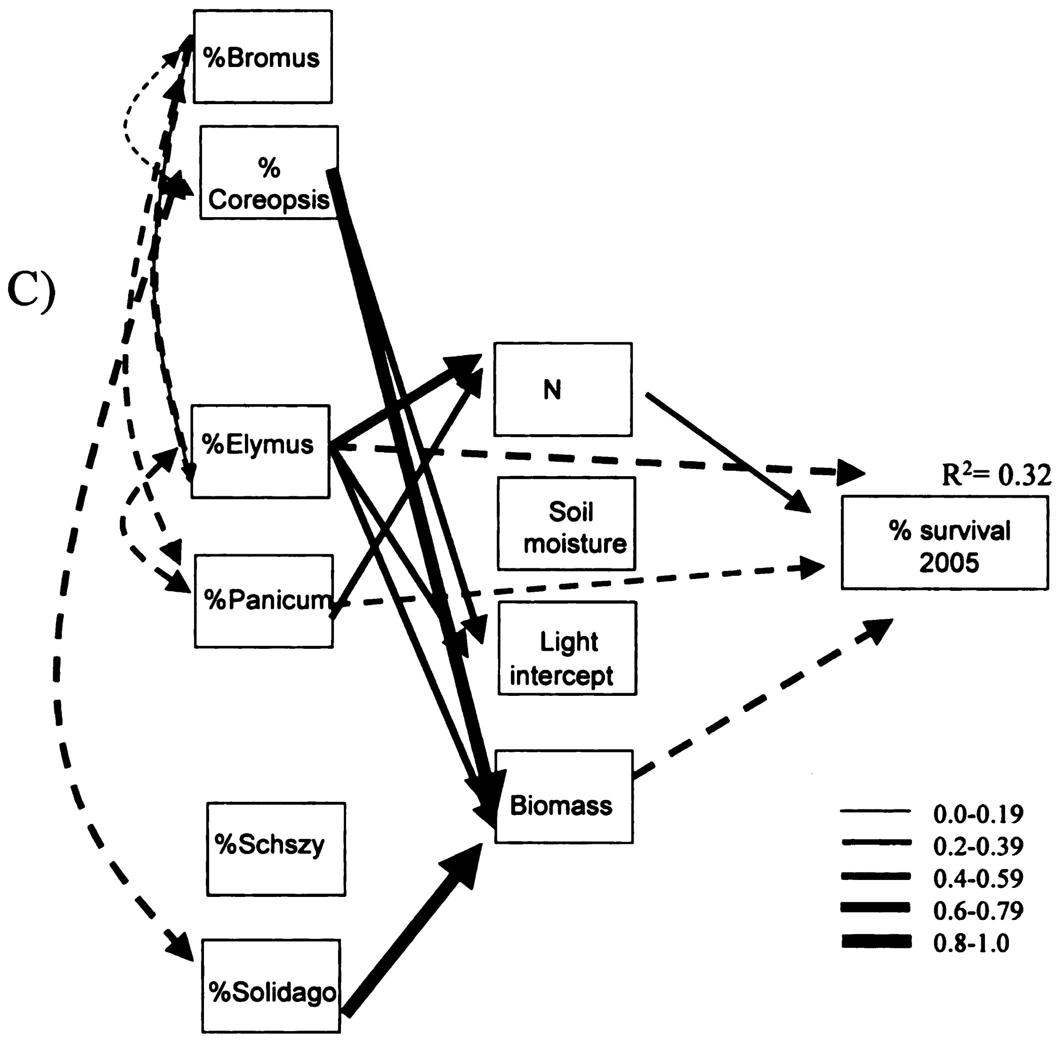


Figure 4.5c. SEM model for predicting survival of seedling invaders through 2005. Non-significant paths are not shown. Line thickness represents standardized regression weights. Positive relationships are shown with solid lines; negative relationships are in dashed lines.

Table 4.2. Standardized total, indirect, and direct effects of variables in SEM on the three different measures of invasibility.

Variable	**Total Effects**	**Indirect Effects**	**Direct Effects**
On total # seedlings			
%*Bromus*	-0.63	-0.27	-0.35
%*Coreopsis*	-1.0	-0.52	-0.55
%*Elymus*	-0.87	-0.40	-0.47
%*Panicum*	-0.26	0.02	-0.27
%*Schizachrium*	-0.65	-0.23	-0.43
%*Solidago*	-0.62	-0.33	-0.28
Biomass	-0.35		-0.35
Light interception	-0.39		-0.39
Nitrogen	0.04		0.04
Soil moisture	0.11		0.11
On seedling species richness			
%*Bromus*	-0.54	-0.20	-0.34
%*Coreopsis*	-1.0	-0.42	-0.59
%*Elymus*	-0.66	-0.31	-0.35
%*Panicum*	-0.18	0.03	-0.21
%*Schizachrium*	-0.56	-0.18	-0.39
%*Solidago*	-0.45	-0.27	-0.18
Biomass	-0.30		-0.30
Light interception	-0.32		-0.32
Nitrogen	0.08		0.08
Soil moisture	0.14		0.14
On seedling survival			
%*Bromus*	-0.25	0.06	-0.40
%*Coreopsis*	-0.61	-0.16	-0.45
%*Elymus*	-0.53	-0.00	-0.53
%*Panicum*	-0.19	0.15	-0.35
%*Schizachrium*	-0.39	0.08	-0.47
%*Solidago*	-0.45	-0.20	-0.25
Biomass	-0.40		-0.40
Light interception	0.10		0.10
Nitrogen	0.31		0.31
Soil moisture	0.14		0.14

negatively related to survival.

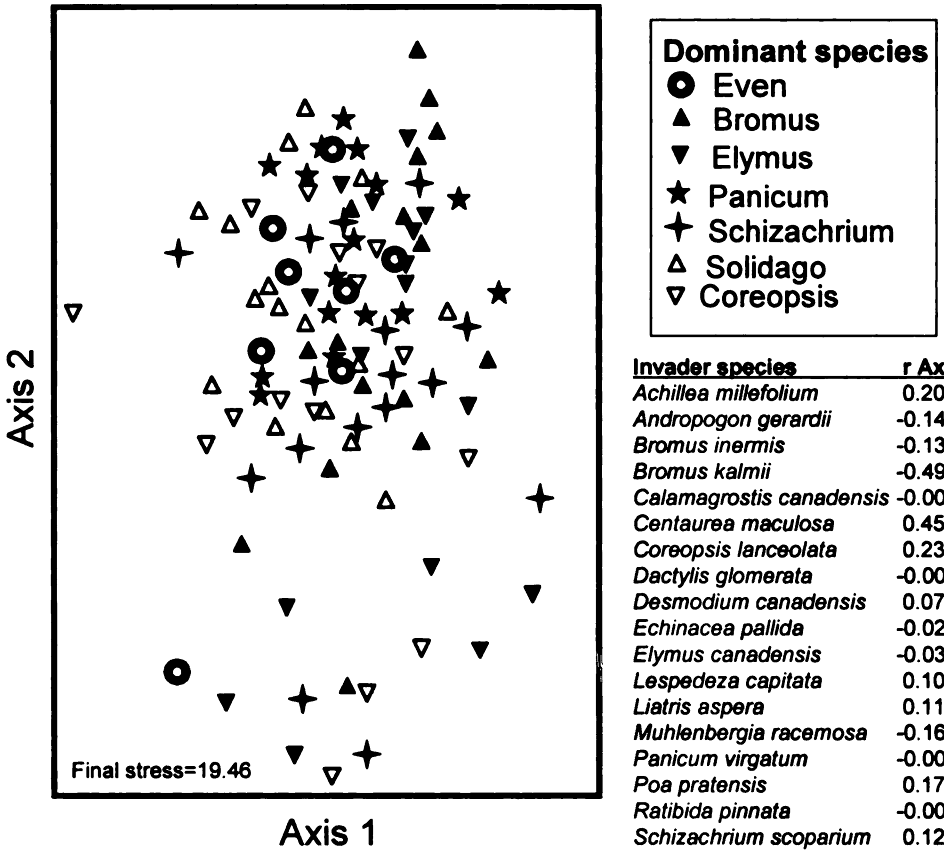
Invader composition

The MRPP analysis showed that there were significant among the dominant-species treatments in the composition of species that invaded them (overall p=0.002). *Schizachrium*-dominated pots had significantly different seedling invader composition from *Panicum* and *Solidago* pots (Table 4.3).

The NMS ordination reduced the dimensionality of the composition of invaders to two axes (Figure 4.6). Together, these two axes explained 85% of the variation in invader composition among the pots (axis 1= 9.8%, axis 2=75.5%). We used the two axis scores for each pot as variables describing the invader composition (see Figure 4.6 for correlations of each invader species with each axis). Axis 1 was related negatively to *Bromus kalmii* seedlings and positively to *Centaurea maculosa* seedlings, while Axis 2 seemed related to several invader species, including *Centaurea*, *Dactylis glomerata*, and *Schizachrium scoparium*. The SEM relating intact species abundance, resources, and pot scores for Axis 1 and Axis 2 (i.e. invader composition) is shown in Figure 4.7. 19% of variation in Axis 1, and 49% of variation in Axis 2 was explained by the model. In this model, all species were significant predictors of invader composition, and most had both direct and indirect effects (Table 4.4), though most direct effects were predicting variation in Axis 1 scores (i.e. success of *Bromus kalmii* and *Centaurea*). Nitrogen was also positively related to Axis 1 (i.e. negatively to *Bromus kalmii* success). Variation in Axis 2

Table 4.3. Results from multi-response permutation procedure. Uncorrected P-values are shown, but Bonferonni corrected significant comparisons at p=0.003 (0.05/15) are starred (*)

Comparison	**A (effect size)**	**p**
All Groups	0.069	0.002*
Bromus vs. *Coreopsis*	0.053	0.06
Bromus vs. *Elymus*	-.022	0.80
Bromus vs. *Panicum*	0.04	0.05
Bromus vs. *Schizachrium*	0.03	0.11
Bromus vs. *Solidago*	0.04	0.07
Coreopsis vs. *Elymus*	0.02	0.21
Coreopsis vs. *Panicum*	0.11	0.01
Coreopsis vs. *Schizachrium*	0.02	0.17
Coreopsis vs. *Solidago*	0.05	0.07
Elymus vs. *Panicum*	0.045	0.045
Elymus vs. *Schizachrium*	-0.002	0.42
Elymus vs. *Solidago*	0.04	0.06
Panicum vs. *Schizachrium*	0.11	0.003*
Panicum vs. *Solidago*	0.02	0.15
Schizachrium vs. *Solidago*	0.11	0.001*



Invader species	r Axis1	r Axis2
Achillea millefolium	0.204	0.336
Andropogon gerardii	-0.144	0.212
Bromus inermis	-0.134	0.283
Bromus kalmii	-0.495	0.442
Calamagrostis canadensis	-0.008	0.041
Centaurea maculosa	0.450	0.715
Coreopsis lanceolata	0.237	0.485
Dactylis glomerata	-0.003	0.804
Desmodium canadensis	0.073	0.468
Echinacea pallida	-0.027	0.171
Elymus canadensis	-0.038	0.521
Lespedeza capitata	0.109	0.505
Liatris aspera	0.116	0.405
Muhlenbergia racemosa	-0.163	0.400
Panicum virgatum	-0.003	0.568
Poa pratensis	0.171	0.147
Ratibida pinnata	-0.004	0.098
Schizachrium scoparium	0.121	0.612
Solidago nemoralis	0.056	0.182

Figure 4.6. Non-metric multidimensional scaling ordination of seedling invader data shown on two axes which together explain 85% of the variation in seedling data. Each pot is plotted, and identified based on its dominant species. Correlation values between each invader species and the two axes are also shown.

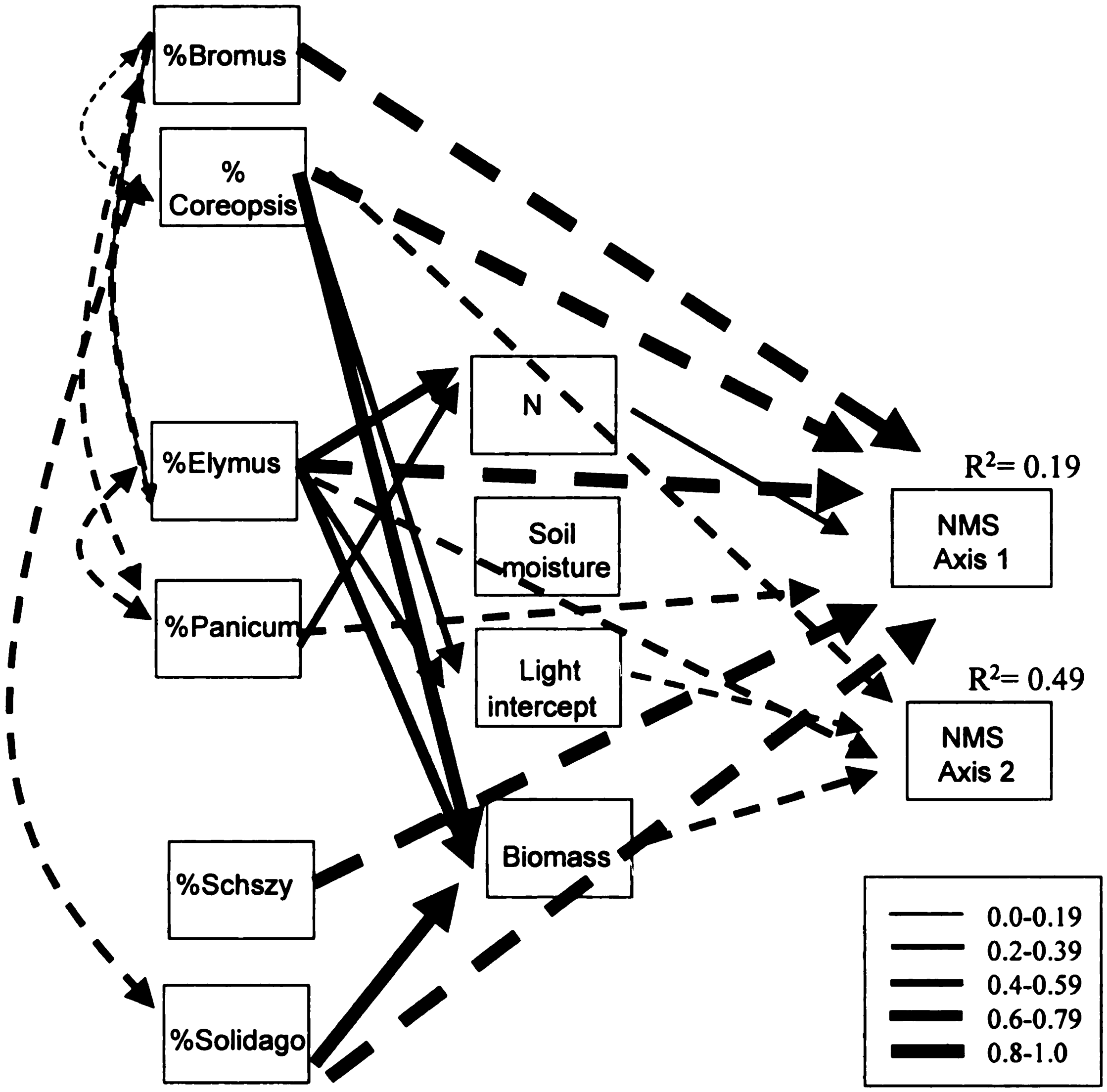


Figure 4.7. SEM for NMS axes scores summarizing invader composition. Numbers above invisibility measures are R^2 values. Non-significant paths are not shown. Line thickness represents standardized regression weights. Positive relationships are shown with solid lines; negative relationships are in dashed lines.

Table 4.4. Standardized total, indirect, and direct effects of variables in SEM on the two NMS axes scores summarizing invader composition.

Variable	Total Effects	Indirect Effects	Direct Effects
On Axis 1 scores			
%*Bromus*	-0.76	0.11	-0.86
%*Coreopsis*	-0.89	0.06	-0.95
%*Elymus*	-0.75	0.12	-0.87
%*Panicum*	-0.35	0.13	-0.47
%*Schizachrium*	-0.61	0.10	-0.71
%*Solidago*	-0.97	0.05	-1.0
Biomass	-0.06		-0.06
Light interception	0.02		0.02
Nitrogen	0.26		0.26
Soil moisture	0.10		0.10
On Axis 2 scores			
%*Bromus*	-0.76	0.11	-0.40
%*Coreopsis*	-1.0	0.06	-0.55
%*Elymus*	-0.95	0.12	-0.51
%*Panicum*	-0.28	0.13	-0.29
%*Schizachrium*	-0.66	-0.21	-0.45
%*Solidago*	-0.64	-0.45	-0.20
Biomass	-0.43		-0.43
Light interception	-0.26		-0.26
Nitrogen	0.02		0.02
Soil moisture	0.10		0.10

(i.e. success of *Centaurea*, *Dactylis*, *Schizachrium*, and other species) was negatively related to light, biomass, and direct effects of *Coreopsis* and *Elymus*.

Discussion

This study shows that other aspects of community diversity other than species richness can have significant effects on invasibility of communities. In our experiment, we were able to control species composition, soil, and other factors that might contribute to differential invasion success, allowing us to explicitly examine the effects of species identity and relative abundance (evenness) of a dominant species on invasion. We also found that dominant species identity can affect invasion, even beyond effects on resources like light or nitrogen availability.

Predictors of invasibility

We found that the identity of the dominant species can have strong effects on the invasibility of a community. In our experiment, *Coreopsis*-dominated pots tended to have the lowest invasion, while *Panicum* and *Bromus* pots tended to have the highest invasion rates. *Coreopsis* dominated pots also had the highest aboveground biomass in 2005, and higher than average, but not the highest, biomass in 2004. *Coreopsis* pots also had the lowest available nitrogen. *Panicum* plots tended to have lower biomass and higher light levels than average, but so did a couple of other treatments. *Bromus* pots also did not obviously stand out as different, so again it is not clear why these two treatments should have high invasibility.

From the SEM analyses, it appears that light reduction during seedling emergence (May), as well as community aboveground biomass, plays an important role in reducing invasibility of communities at early stages of invasion. Light availability and community biomass also explained most of the variation among pots in seedling survival in 2005. These results are consistent with findings of several other studies that light availability is a major factor regulating seedling establishment (Tilman 1993, Jutila and Grace 2002, Hofmann and Isselstein 2004). Further, aboveground biomass (and litter) production are known to negatively impact seedling establishment, by both decreasing light and increasing competition, at least in habitats where water is not often limiting (Foster and Gross 1998, Foster 1999, Maret and Wilson 2005). One treatment in our study (*Solidago*-dominated) had high early light availability, but also had the highest late-season aboveground biomass, which may have negated the advantage to seedlings of high early light by increasing competition with the intact community later in the season (e.g., Humphrey and Schupp 2004, Cipriotti and Aguiar 2005). We saw no effect of soil moisture, which is consistent with other studies that have found that water availability is usually only a limiting factor for seedlings in dry or Mediterranean climates (Garcia-Serrano et al. 2004). While we did see differences in nitrogen availability among treatments, this had no detectable effect on first year seedling establishment. Second year seedling survival was higher in pots with more available nitrogen, though this effect was not as strong as the effects of light and biomass. While nitrogen availability has been found to be important in predicting community invasions (e.g., Prieur-Richard et al. 2002), this is usually in the context of success of transplanted seedlings, not initial establishment of individuals from seeds. Like this study, others have shown no effect of nutrients such as nitrogen or phosphorus on initial establishment of seedlings (e.g., Ganade and Brown 2002).

The significance of direct effects of individual species on invasibility indicates that there may be other factors influencing invasion success of seedlings that we did not measure in this study. For example, intact plant communities can alter soil biota communities that may have strong effects on seedling success (e.g., van Ruijven et al. 2003). In particular, recent research has shown that differences in mycorrhizal communities can have large impacts on seedling establishment in grasslands (e.g., Moora and Zobel 1998, van der Heijden 2004), though in some cases competition with established mycorrhizal plants may negate any benefits of mycorrhizae for seedlings (Kytoviita et al. 2003). In general, though, belowground processes are a black-box for much of community ecology. Fine root volume or rooting structure may be more important for understanding competition for water and nutrients (Fargione and Tilman 2005). While root biomass was not different among our treatments, active root volume or rooting profiles may well be. Insect and mollusk herbivory are other factors we were unable to control or quantify in our study. Exclusion studies of mollusk herbivores have shown impacts on seedling survival (e.g., Edwards et al. 2005), and other diversity studies have shown effects of plant composition on insect composition (e.g., Knops et al. 1999), which may indirectly impact seedlings (Prieur-Richard et al. 2002).

Community evenness and invasibility

Surprisingly, community evenness had little effect on invasibility in our study. From other studies (e.g., Wilsey and Polley 2002, Tracey and Sanderson 2003), we expected that increased evenness would decrease invasibility of communities. The EVEN treatment had no more or fewer initial numbers of invaders than the treatments dominated by different species. When looking at initial planted evenness of all pots, we again found no relationship between evenness and invasion. When examining the actual evenness of mesocosms as they shifted over the two years of the study, we found a slight positive relationship between evenness and invasibility, but this only explained 5% of the variation in invader recruitment, and relationships within dominant-species were either non-significant (4/6 species), or in opposite directions. The only indication that evenness may be important in this study was in the second-year survival of invader, where survivorship was lower in the even treatment than in the other treatments.

Relative importance of species identity

Very few studies have examined the role of species identity and evenness explicitly on invasion, and so it is unknown how important these aspects of diversity are relative to species richness, which has been examined exhaustively. In most studies of species richness-invasibility relationships, the effect size for differences in invasion at low and high species richness is often only a few invader species. For example, Fargione et al. (2003) added 27 species as seeds to plots with 1-24 resident species. While invasibility decreased with increased plot species richness, the change was from an average of five successful invading species to an average of two successful invading species. Van Ruijven and others (2003) conducted an experiment manipulating community species richness between one and eight species, and found that the number of successful invading species across treatments differed by no more than five species. At the English site for the BIODEPTH experiment Hector et al. (2001), varied community species richness from one to 11 species, while the number of successful invading species varied only between five and seven. When invasibility is quantified as the number of successful individuals establishing from a seed addition, differences among diversity treatments often range between 5-15% establishment success (e.g., Levine 2000, Prieur-Richard et al. 2000, Lyon and Schwartz 2001, Smith et al. 2004). At least one study claimed to show a significant effect of community species richness (1-15 species) on invasion, though treatments varied between an average of two to four invading individuals from 1500 added seeds (Lindig-Cisneros and Zedler 2002). In our study, the range of successful invading species varied from an average of seven in *Coreopsis*-dominated plots to an average of 13 in *Panicum*-dominated plots. Establishment of individuals ranged from 3-7% across treatments in 2004. While we do not have treatments that varied in species richness to compare directly, the effects of dominant species in our experiment is comparable, if not stronger, than effects of species richness found in other studies.

Conclusions

With this study, we have been able to explicitly examine the role of dominant species identity and relative abundance on invasibility of communities. We found that the identity of certain dominants, but not community evenness, can have significant impacts on invasibility. In fact, the magnitude of effect that dominant species identity has on invasion is similar or greater than that of other studies examining relationships between community species richness and invasion. While we have shown that dominant species affected success of invaders in our study by altering light availability and community biomass, there are other potential mechanisms, especially biotic and belowground interactions, by which dominant species may affect invasibility that deserve further exploration.

CHAPTER 5

LITTLE EVIDENCE FOR LIMITING SIMILARITY BETWEEN INVADERS AND DOMINANTS IN GRASSLAND PLANT COMMUNITIES

Abstract

To understand invasion, ecologists ask two questions: what makes a good invader? and what makes a community invasible? Few studies have combined both questions to understand which invaders are successful in which communities. Limiting similarity theory offers the prediction that successful invaders should be functionally different from species already in the community. Because dominant species are known to have strong effects on ecosystem functioning, I hypothesized that successful invaders should be functionally dissimilar from community dominants. To test this, I added seeds of 17 different species to two different experiments: one in a natural oldfield community that had patches dominated by different plant species, and one in mesocosms of planted grassland species that varied in the identity of the dominant species, but not in species richness or evenness. The majority of invader species showed no variability in success, and there was no consistent pattern among those species that did show differences in establishment and survival among communities dominated by different species, suggesting that mechanisms of limiting similarity are not commonly driving invasibility of these communities. Further, there were differences in the absolute success of different functional groups of invaders (C3 grasses, C4 grasses, and forbs), and non-native invaders were much more successful as establishing than native invaders overall, suggesting that results from experiments using a single species of invader should be interpreted with caution.

Introduction

Two questions are fundamental to understanding invasion: what makes a good invader? and what makes a community invasible? Most studies investigating processes of invasion have focused on either characterizing traits of successful invaders (e.g., seed size or competitive ability; Rejmanek and Richardson 1996, Sharma et al. 2005), or characterizing attributes of a community that make it susceptible to invasion (e.g., species diversity or primary productivity; Shea and Chesson 2002, Levine et al. 2004). There have been few studies that have considered aspects of both invaders and communities to understand what types of invaders are most successful in different communities. In fact, most studies quantify the invasibility of an entire community based on the performance of a single invader species -- often a noxious non-native weed (e.g., Naeem et al. 2000, Dukes 2001, Prieur-Richard et al. 2002).

Despite the paucity of studies addressing both potential invaders and susceptible communities, ideas concerning potential relationships between traits of successful invaders and invaded communities have been around for quite some time. In *The Origin of Species*, Darwin (1859) laid out his Naturalization Hypothesis, which predicted that invaders in the same genus as species already present in a system should be less likely to successfully colonize than species from different genera due to competition for similar habitats (Daeler 2001). More recently, both niche complementarity and "limiting similarity" theory (Tilman 1982, Abrams 1983, Silvertown 2004) have been used as the bases of predictions for understanding the relationships between potential invaders and different communities: One prediction is that species already present in the community should suppress invasion by functionally similar species that have similar resource requirements (Fargione et al. 2003, Tilman 2004). In other words, communities may be invasible if there are no species that are ecologically similar to the invader (Lodge 1993, Stubbs and Wilson 2004).

Because dominant species in communities are known to have strong regulating effects on community structure and ecosystem function (McNaughton and Wolf 1970, Crawley et al. 1999), it is likely that dominant species in a community exert strong influence on the type of species that is a successful invader. A few recent studies in synthetic, experimental communities have shown that species that are functionally dissimilar to the dominant species in communities are more likely to successfully invade than similar species. For example, van Ruijven et al. (2003) showed that an aster invader was negatively affected by the presence of a dominant aster species in an experimental community, beyond other effects of diversity. Similarly, Xu et al. (2004) found that forb-dominated communities were most resistant to invasion by alligator weed (*Alternanthera philoxeroides*), another forb. Other studies within a given community type, in systems from prairies to ant assemblages, also indicate that successful colonizers are generally functionally dissimilar to the dominant species (Cully et al. 2003, Gibb and Hochuli 2003).

However, not all studies have found evidence for limiting similarity influencing invasion success within community types. In two experiments involving removal of functional groups from intact communities, there were no relationships between community composition and type of successful invader (Symstad 2000, Von Holle and Simberloff 2004). At least one study, using synthetic communities, found that successful invaders were functionally similar to the dominant species, possibly due to the dominant species ‘protecting’ seedlings from herbivory, with insects concentrated on the dominant species, leaving seedlings alone (Prieur-Richard et al. 2002).

Despite the insight gained from the studies described above, there has been some concern about the ability to make generalizations about invasion of natural communities from experimental studies in synthetic communities, especially when species richness of communities is manipulated (Wardle 2001). Several factors, including sampling effects and disturbance can confound interpretation of results from these experimental communities. To explicitly examine relationships between traits of dominant species and successful invaders, it is necessary to design experiments that manipulate identity of dominant species without altering species richness or disturbance intensity. Further, because natural communities assemble differently than experimental communities (e.g. Ricklefs 2004), there is a need for experiments in natural systems to address relationships between community composition and successful invader composition. In this study, I examined these relationships in two experiments. The first experiment was conducted in natural oldfield plant communities that had distinct vegetation patches that differed in the identity of the dominant species. The second experiment involved constructed plant communities that varied in the identity of the dominant species, but not in species richness or evenness. To both systems, I added seeds of 17 different species, spanning a range of nativity and functional types, to examine the performance of these different invaders as a function of the identity of the dominant species. Specifically, I asked the question: Are invaders that are functionally dissimilar to the dominant species more likely to succeed than other species? I also examined whether non-native species were more likely to invade than native species, in order to frame results from this study in the context of other studies of community invasibility.

Methods

Experimental Design: Natural oldfields

In March of 2004, I established 64 1m x 1m plots in patches of vegetation dominated by one of four different species - *Andropogon virginicus* (native C4 grass), *Bromus inermis* (non-native C3 grass), *Centaurea maculosa* (non-native forb), or *Solidago canadensis* (native forb) -.across one oldfield near the W.K. Kellogg Biological Station (KBS) in SW Michigan (Lux Arbor Reserve, Barry County; 42.2833°N, 85.2768°W) (see chapter 3 for details). I haphazardly distributed a total of 16 plots in patches dominated by each dominant species. In August, I determined species composition and abundance in each plot using visual estimates of percent cover of each species. Plot species richness was calculated from these visual estimates of community composition.

Experimental Design: Constructed community mesocosms

I conducted a mesocosm experiment outdoors at the W.K. Kellogg Biological Station (KBS) in SW Michigan, USA (Kalamazoo County; 42.2460°N, 85.2359°W) from July of 2003-September 2005 (see chapter 4 for design details). In September 2003, I transplanted a total of 48 plugs per pot using eight species common to Midwest US grasslands and known to be dominants in some areas within the region (Table 5.1) to create 6 treatments that varied in the identity of the dominant, but not in species richness or evenness (34:2:2:2:2:2:2:2 planting ratio). Six of the eight species were rotated as dominants (all but *Desmodium* and *Lespedeza*). Planting arrangements were randomized within each pot. Each treatment was replicated eight times (48 pots total). All plugs were grown from seed in the greenhouse during June 2003, and transferred outside under shadecloth and regularly watered in July and August. After transplanting, pots were regularly watered for two weeks to help establishment, and then left alone through the fall and winter. In early May 2004, I weeded the pots to remove winter annual species that had germinated from the seedbank or from dispersal into the pots. Individuals were removed from pots by clipping stems with small scissors just below the soil surface to minimize soil disturbance.

Seed Addition

In March 2004, I added 50 seeds of 17 different species, all common to Michigan grasslands and oldfields (Rabeler 2001) and representing a variety of functional types and nativity (Table 5.1) to a 0.25m x 0.5m subsection in each m^2 plot in the field experiment (the rest of the plot was undisturbed or used for other experiments), and 50 seeds of each species to each pot in the mesocosm treatment. I classified the invader species into three functional groups: C3 (cool season) grasses, C4 (warm season) grasses, and forbs, based on phenology and growth form. Species were classified as native or non-native to North America based on information from the USDA PLANTS Database (http://plants.usda.gov). Seeds were added in early spring (March) to take advantage of possible freeze/thaw requirements needed for germination. Seeds of native species were purchased from a native-plant grower in Minnesota (Prairie Moon Nursery, Winona,

Table 5.1. Species added as seeds to experiments (field and mesocosm). Origin refers to North American presence. Species in bold are the eight species transplanted to create initial communities in the mesocosm experiment.

Species	Life Form	Origin
Achillea millefolium	forb	native
Andropogon gerardii	C4 bunchgrass	native
Bromus inermis	**C3 clonal grass**	**non-native**
Bromus kalmii	C3 bunchgrass	native
Calamagrostis canadensis	C3 clonal grass	native
Centaurea maculosa	forb	non-native
Coreopsis lanceolata	**forb**	**native**
Dactylis glomerata	C3 bunchgrass	non-native
Echinacea pallida	forb	native
Elymus canadensis	**C3 clonal grass**	**native**
Liatris aspera	forb	native
Muhlenbergia racemosa	C4 clonal grass	native
Panicum virgatum	**C4 clonal grass**	**native**
Poa pratensis	C3 clonal grass	non-native
Ratibida pinnata	forb	native
Schizachyrium scoparium	**C4 bunchgrass**	**native**
Solidago nemoralis	**forb**	**native**

MN), non-native grass seeds were purchased from a forage crop seed supplier (Michigan State Seed Solutions, Grand Ledge, MI), and *Centaurea maculosa* seeds were collected from nearby fields. All species were also sown into outdoor common gardens to confirm seed viability. In August 2004, I determined what species had established in the plots by counting seedlings. For the field experiment, I also censused seedlings in adjacent control subplots of the same size to quantify natural invasion from the local community. I used the difference in seedling number between seed-added and control plots to quantify invasion of each added species in each patch type.

In order to examine second-year invader survival of invaders, the mesocosm experiment was extended through 2005. Seedlings censused in pots in 2004 were marked with toothpicks, and survival of seedlings censused in 2004 was recorded in August 2005. Seedlings in the field experiment were not marked, and so it was impossible to follow second-year survival in that experiment.

Data Analyses

To determine effects of dominant species on invasion success of different functional groups in the field experiment, I used an Analysis of Covariance (ANCOVA) with dominant patch type as the main effect. Because of known relationships between diversity and invasion from other studies, I used plot species richness as a covariate in the ANCOVA. For the mesocosm experiment, I used one-way Analysis of Variance (ANOVA) with dominant species as the main factor. For both the field and mesocosm experiments, I also used ANOVA to compare relative establishment success of native and non-native invaders. Establishment and survival percentages of seedlings were arcsine square root transformed for analyses to better meet normality assumptions. All ANOVA analyses were performed using Systat v. 11 (SYSTAT Software, Inc. 2004).

I used indicator species analysis (Dufrene and Legendre 1997, McCune et al. 2002, p. 198) to examine whether individual invading species showed differences in their establishment success across communities dominated by different dominant species. Indicator species analysis involves calculating a metric that summarizes both the relative abundance and frequency of each species in each treatment such that:

$$IV = RA_{kj} \times RF_{kj} \times 100.$$

Where RA is the relative abundance of a given species j (i.e., a species added as seed) in a given group k (i.e., a dominant species treatment) and RF_{kj} is the proportional frequency of species j in group k (i.e., the proportion of plots in each treatment that contain species j). Values range from 0 (no indication for any patch type) to 100 (perfect indication). The observed IV is compared to an expected IV calculated using Monte-Carlo randomizations of the data, where species frequency and abundance data from each plot is randomly assigned to a group/treatment 1000 times. The null hypothesis is that the observed IV is no larger than would be expected by chance (i.e. a species has a '0' indicator value). Since this analysis only determines in which treatment each species does 'best', I also used seedling failure data (i.e., 50 seeds added – the number of surviving seedlings) for each species to similarly calculate in which treatments each invader species did 'worst'. Similarly, I used 2005 invader survival data from the mesocosm experiment to calculate in which treatments each invader species survived the best or worst. I also summarized invader species and dominant species into functional groups, to see in which dominant functional group treatment each invader functional group did best and worst. The indicator species analyses were performed in PC-ORD (McCune & Mefford 1999).

Results

Functional Groups

Overall, across all dominant patch types in the field experiment, C4 grasses were least successful in invading ($F_{2,165}$=24.7, p<0.001). Within each functional group, C4 grasses were more successful in *Centaurea* patches than in *Bromus* patches ($F_{3,55}$=3.11; p=0.034; Figure 5.1). Forbs and C3 grasses had higher establishment success than C4 grasses in general, but showed no differences in colonization success among patch types (forbs: $F_{3,55}$=0.173; p=0.914; C3: $F_{3,55}$=0.697; p=0.558; Figure 5.1).

In the mesocosm experiment, there were no significant differences in establishment success among functional groups when examined across all dominant species treatments ($F_{2,192}$=0.30, p=0.74). However, second-year survival of seedlings was greater for C3 grasses than forbs or C4 grasses across all treatments ($F_{2,182}$=5.34, p=0.006). Within each functional group, C4 grasses had higher establishment success in *Panicum* and *Solidago* pots than in *Schizachrium* pots ($F_{5,48}$=2.94, p=0.023), though second-year survival did not differ among treatments ($F_{5,45}$=2.29, p=0.064; Figure 5.2). For C4 grasses, pots dominated by *Panicum* had higher establishment than pots dominated by *Coreopsis* ($F_{5,48}$=3.70, p=0.007), though again second-year survival did not differ among treatments ($F_{5,48}$=2.27, p=0.064; Figure 5.2). Forbs were more successful at establishing in *Bromus* and *Panicum* pots than in *Coreopsis* pots ($F_{5,48}$=4.45, p=0.002),

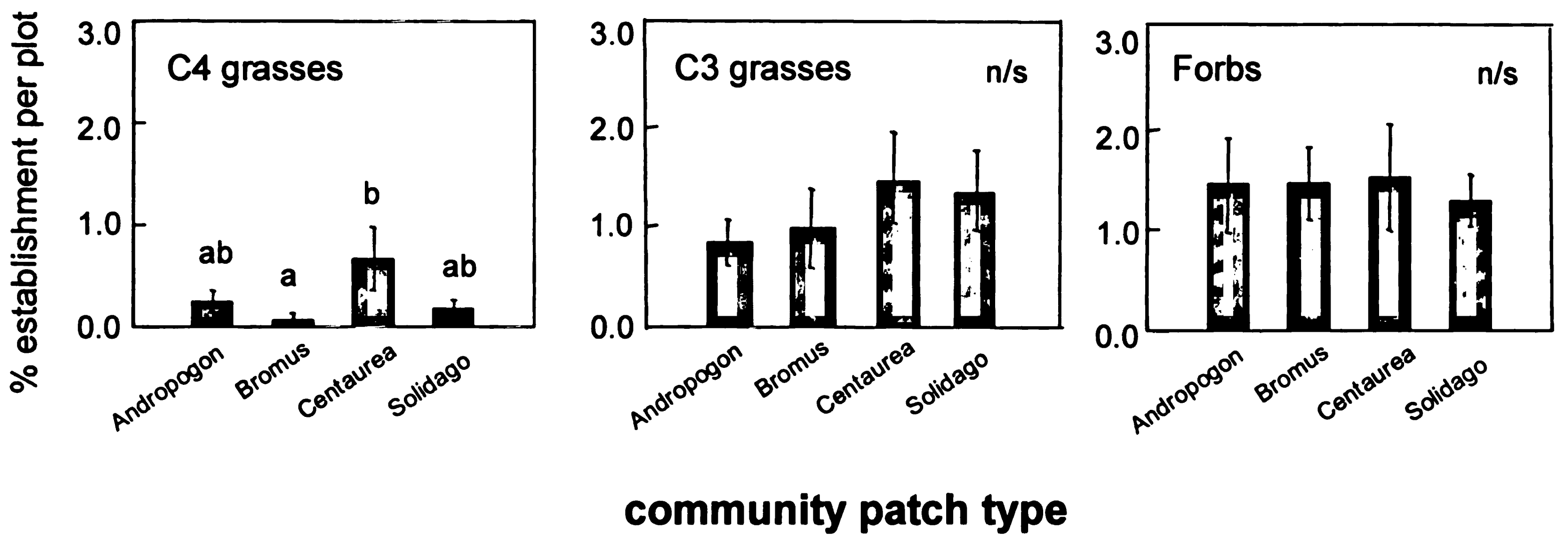


Figure 5.1. Relative establishment success of the different invader functional groups in the different dominant patch types in the field experiment. Bars represent one standard error. Letters indicate significant differences at the $p<0.05$ level in the ANCOVA model with Tukey adjustments for multiple comparisons.

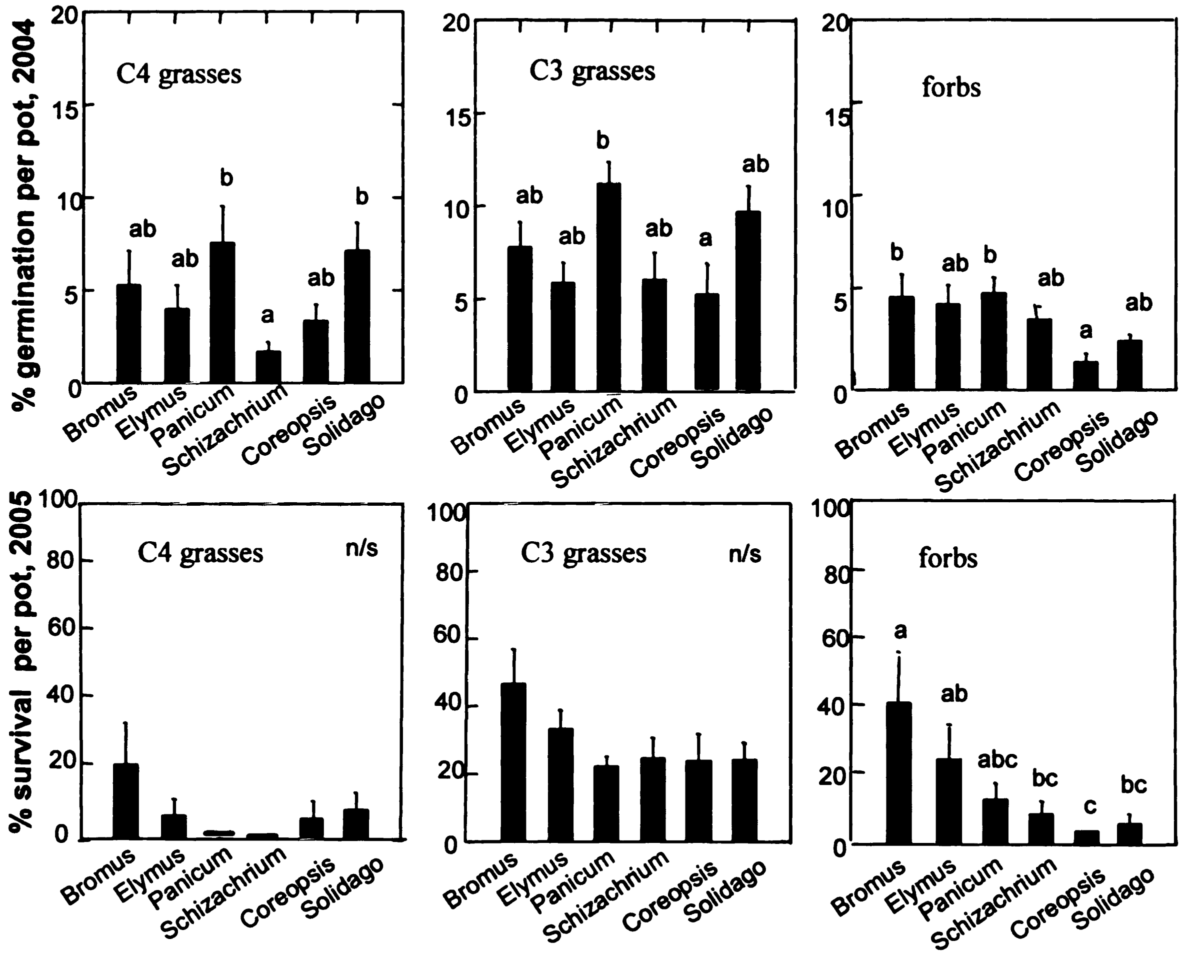


Figure 5.2. Relative establishment (2004) and two-year survival (2005) success of the different invader functional groups in the different dominant species treatments (on X-axis) in the mesocosm experiment. Bars represent one standard error. Letters indicate significant differences at the $p<0.05$ level in the ANOVA model with Tukey adjustments for multiple comparisons.

while second-year survival was higher in *Bromus* pots than *Schizachrium*, *Coreopsis*, or *Solidago* pots ($F_{5,47}$=6.92, p<0.001; Figure 5.2).

Native vs. Non-native invaders

In all patch types in the field experiment, non-native species had significantly higher establishment success than native species ($F_{1,110}$=53.45, p<0.001; Figure 5.3), though there were no differences in establishment success among dominant patch types for either native ($F_{3,55}$=1.29, p=0.288) or non-native invaders ($F_{3,55}$=0.871, p=0.462).

In the mesocosm experiment, non-native species again had higher establishment ($F_{1,96}$=134.82, p<0.001) and survival ($F_{1,95}$=32.86, p<0.001) rates than native species (Figure 5.4). Further, native species had higher establishment success in *Panicum* and *Solidago* pots than in *Schizachrium* pots ($F_{5,48}$=3.25, p=0.014), while second-year survival was greater in *Bromus* than in *Panicum* or *Schizachrium* pots ($F_{5,48}$=3.78, p=0.006). Non-native species had higher establishment success in *Bromus* and *Panicum* than in *Coreopsis* pots ($F_{5,48}$=3.37, p=0.012), and second-year survival was greater for non-natives in *Bromus* pots than in *Coreopsis* or *Solidago* pots ($F_{5,47}$=3.09, p=0.019).

Indicator Species Analysis

Only six of the 17 species added as seeds in the field experiment showed any differentiation in establishment success among the different patch types (Table 5.2). *Echinacea pallida*, a forb, showed significant affinity with *Bromus*/C3 grass communities, and was significantly least successful in *Solidago* communities. *Schizachrium scoparium,* a C4 grass, showed significant affinity with *Centaurea*

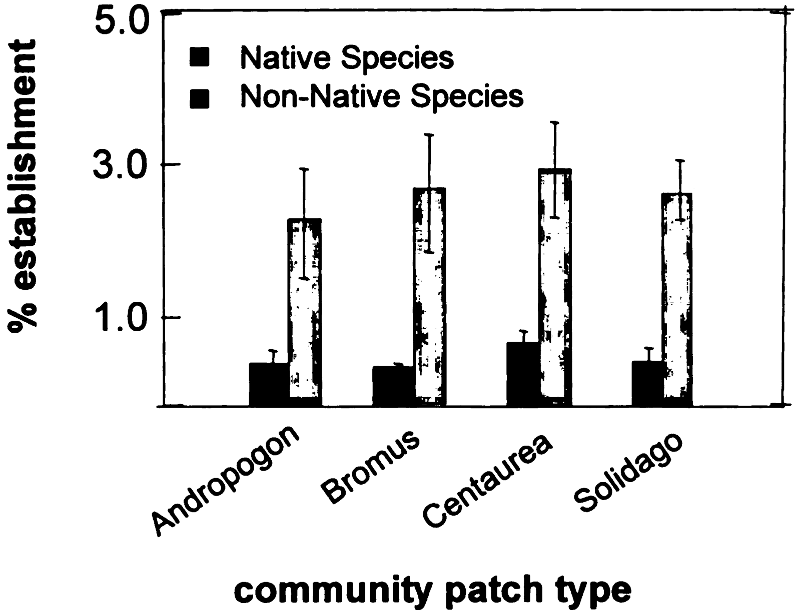


Figure 5.3. Relative establishment success of native and non-native invaders in the field experiment. Bars indicate one standard error.

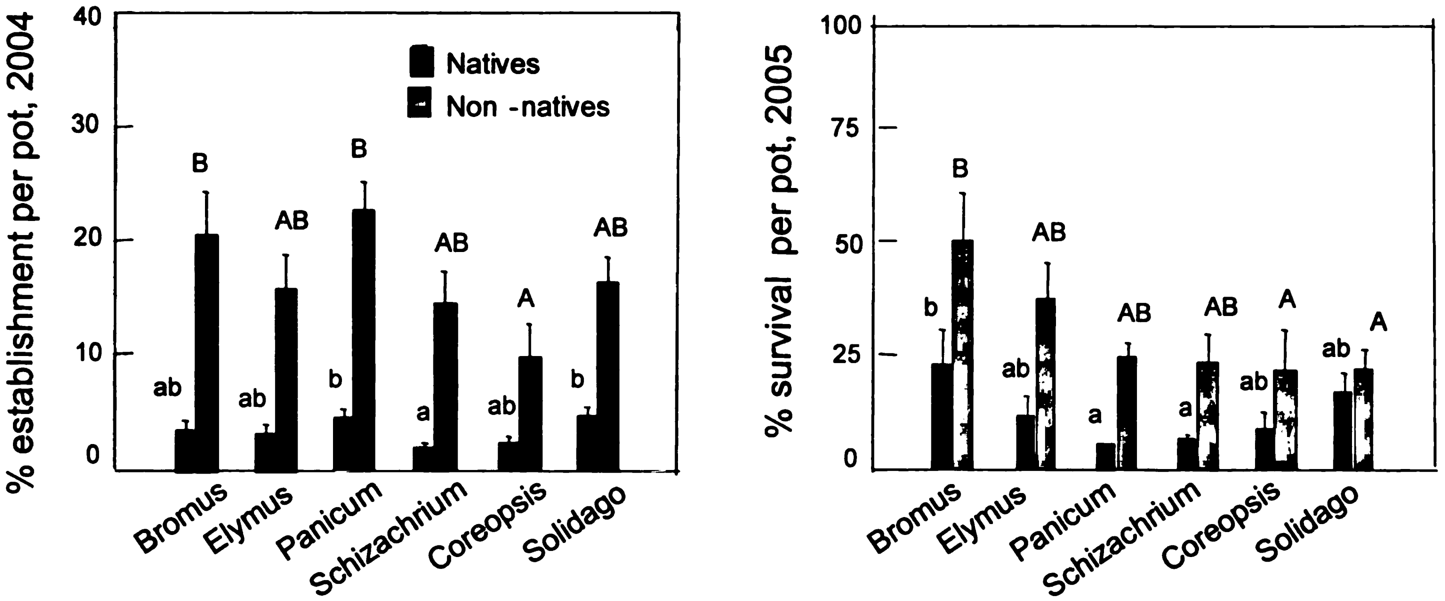


Figure 5.4. Relative establishment (2004) and two-year survival (2005) success of native and non-native invaders in the different dominant species treatments (on X-axis) in the mesocosm experiment. Bars represent one standard error. Letters indicate significant differences across treatments within each invader group at the $p<0.05$ level in the ANOVA model with Tukey adjustments for multiple comparisons.

Table 5.2. Results from the indicator species analysis for the field experiment. Species are grouped by functional group. Significant relationships between each invader species (or functional group) and the community dominant (species or functional group) are shown for both greatest establishment ('high group') and lowest establishment ('low group'). Significance values are calculated based on 1000 randomizations in a Monte Carlo simulations, with * p<0.10, ** p<0.05, and *** p<0.01.

	By dominant species: 2004 establishment		**By dominant functional group: 2004 establishment**	
Species	**high group**	**low group**	**high group**	**lowgroup**
B. inermis	n/s	n/s	C3 grass**	n/s
B. kalmii	n/s	*Bromus***	n/s	C3 grass*
C. canadensis	n/s	n/s	n/s	n/s
D. glomerata	n/s	*Bromus***	n/s	C3 grass**
E. canadensis	n/s	n/s	n/s	n/s
P. pratensis	n/s	*Bromus***	n/s	C3 grass*
C3 grasses	n/s	n/s	n/s	n/s
A. gerardii	n/s	n/s	n/s	n/s
M. racemosa	n/s	n/s	n/s	n/s
P. virgatum	n/s	n/s	n/s	n/s
S. scoparium	*Centaurea***	n/s	n/s	n/s
C4 grasses	n/s	n/s	n/s	n/s
A. millefolium	n/s	n/s	n/s	n/s
C. maculosa	n/s	n/s	n/s	n/s
C. lanceolata	n/s	n/s	n/s	n/s
E. pallida	*Bromus***	*Solidago**	C3 grass***	n/s
L. aspera	n/s	n/s	n/s	n/s
R. pinnata	n/s	n/s	n/s	n/s
S. nemoralis	n/s	n/s	n/s	n/s
forbs	n/s	n/s	n/s	n/s

communities, but did not do significantly worse in any one patch type. Three C3 grasses (*Bromus kalmii*, *Dactylis glomerata*, and *Poa pratensis*) all showed highest failure in *Bromus*/C3 grass communities, while another C3 grass (*Bromus inermis*) actually showed highest affinity for C3 grass communities. When invaders were grouped into functional groups, there were no significant associations between invaders and community dominants.

For the mesocosm experiment, nine of 17 species showed some significant association or disassociation in establishment of two-year survival with a dominant treatment (Table 5.3). Establishment and survival of forbs in general showed affinity for *Bromus*/C3 grasses and was lowest in *Coreopsis*/forb treatments, though individual species of forbs did not always match this pattern. For example, *Achillea millefolium* had highest establishment success, but lowest survival success in *Panicum*/C4 grass treatments. C4 grass invaders in general had significantly lower establishment in *Schizachrium* pots, but showed no difference among treatments in second-year survival. Again, though, this was not consistent for all C4 invader species. *Muhlenbergia racemosa*, for example, had the lowest establishment in C3 grass treatments.
Finally, C3 invaders in general had highest establishment success in *Panicum* treatments, and highest survival in *Bromus*/C3 grass treatments, and did not do significantly worse in any one treatment. Only two of six C3 grass invaders showed any differentiation among treatments (*Bromus kalmii* and *Dactylis glomerata*), and these followed the patterns as C3 grasses in general.

Table 5.3. Results from the indicator species analysis for the mesocosm experiment. Species are grouped by functional group. Significant relationships between each invader species (or functional group) and the community dominant (species or functional group) are shown for both greatest establishment or survival ('high groups') and lowest establishment or survival ('low groups'). Significance values are calculated based on 1000 randomizations in a Monte Carlo simulations, with * $p<0.10$, ** $p<0.05$, and *** $p<0.01$. Dashes (--) indicate lack of data to test for relationship.

	By dominant species				By dominant functional group			
	2004 establishment		2005 survival		2004 establishment		2005 survival	
Species	high group	low group	high group	lowgroup	high group	lowgroup	high group	lowgroup
B. inermis	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
B. kalmii	*Panicum***	*Bromus**	n/s	n/s	C4 grass*	C3 grass***	n/s	n/s
C. canadensis	n/s	n/s	--	--	n/s	n/s	--	--
D. glomerata	n/s	n/s	n/s	n/s	n/s	n/s	C3 grass**	n/s
E. canadensis	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
P. pratensis	n/s	n/s	--	--	n/s	n/s	--	--
C3 grasses	*Panicum***	n/s	*Bromus***	n/s	n/s	n/s	C3 grass**	n/s
A. gerardii	n/s	n/s	--	--	n/s	n/s	--	--
M. racemosa	n/s	n/s	--	--	n/s	C3 grass**	--	--
P. virgatum	*Panicum***	*Schizy***	--	--	n/s	n/s	--	--
S. scoparium	*Bromus**	*Schizy***	n/s	n/s	n/s	n/s	n/s	n/s
C4 grasses	n/s	*Schizy****	n/s	n/s	n/s	n/s	n/s	n/s
A. millefolium	n/s	n/s	n/s	*Panicum***	C4 grass**	forb**	C3 grass*	C4grass***
C. maculosa	n/s	*Coreopsis***	*Bromus***	*Coreopsis***	n/s	forb***	C3 grass***	forb***
C. lanceolata	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s
E. pallida	n/s	n/s	--	--	n/s	n/s	--	--
L. aspera	n/s	n/s	n/s	*Panicum**	n/s	n/s	n/s	n/s
R. pinnata	n/s	n/s	--	--	n/s	n/s	--	--
S. nemoralis	n/s	*Coreopsis****	n/s	n/s	n/s	n/s	n/s	n/s
forbs	n/s	*Coreopsis****	*Bromus***	*Coreopsis****	C3 grass*	forb***	C3 grass***	forb***

Discussion

The results from this study show only weak evidence for any predictable relationship between successful invaders and dominant species in communities. Based on mechanisms of limiting similarity, I expected that successful invaders should be functionally different than dominant species in plant communities. However, invaders did not consistently have less success in communities that contained a dominant species in the same functional group as the invader. For example, C4 grass invaders in the mesocosm experiment had the lowest establishment success in pots dominated by *Schizachrium*, a C4 species, as expected with limiting similarity. However, the highest success of C4 invaders was in pots dominated by *Panicum*, another C4 species. The indicator species analysis further showed that the different functional groups of invaders in the field experiment showed no association or disassociation with any one dominant patch type. In fact, only forb invaders in the mesocosm experiment consistently met the predictions of limiting similarity, where forb invaders had lowest establishment and survival success in forb-dominated communities.

Further, I found little evidence for limiting similarity when examining individual species responses across patch types. In the field experiment, only six of 17 species showed any differentiation among patch types as measured by the indicator species analysis. Five of those species had either the closest affinity with dominants that were functionally different (e.g. *Schizachrium scoparium*, a C4 grass, was most closely associated with the *Centaurea* -a forb- patch type) or had a strong disassociation with dominants that were functionally similar (e.g., *Echinacea pallida*, a forb, had lowest establishment in the *Solidago* -another forb- patch type.) In the mesocosm experiment, only nine of 17 species showed any differentiation among dominant treatments, and these differences were even less predictable in terms of limiting similarity. Even establishment and survival of a given invader varied. For example, *Achillea millefolium*, a forb, had the highest establishment affinity with C4 dominants and lowest with forbs, though survival of *A. millefolium* was highest in C3 dominants and lowest in C4/*Panicum* dominant treatments. The majority of species in both experiments showed no difference in affinity across the different dominant treatments.

While the functional group categories I used were general (C3 grasses, C4 grasses, and forbs), phenology and rooting structure differences among these three groups are distinctive, and can promote coexistence of species in different groups. For example, many forbs have taproots that extend below grass root systems, allowing them to access resources not available to more competitive grass species (Raven et al. 1992, p. 471). The coexistence of C3 and C4 grasses in Midwestern U.S. grasslands has been attributed, at least in part, to differences in phenology (Fargione and Tilman 2005 and references therein). Further, the few studies that have examined the relationship between community and invader composition have found some evidence supporting limiting similarity as a mechanism inhibiting invasion of these functional groups (C3/C4/forb). For example, Fargione et al. (2003) found that resident functional groups (C3 grasses, C4 grasses, legumes, and forbs) inhibited invasion from members of their own functional group in experimental communities at Cedar Creek, MN. For future work, it may be more informative to test mechanisms of limiting similarity by examining more specific traits of species (e.g., plant height, specific leaf area, leaf nitrogen content; Stubbs and

Wilson 2004) instead of general functional groups, but this analysis depends on extensive measurements of individuals and is often impractical.

Invasion by non-native species

There has been some attempt to predict and control the spread of invasive species by understanding what types of communities are most susceptible or resistant to invasion. For example, non-native C3 grasses are rapidly invading C4 dominated tallgrass prairie in the U.S. Great Plains (Cully et al. 2003). Management efforts that focus on reintroducing C3 native species (in the same functional group as the invaders) have shown some promise in controlling the spread of these invasive species. Restorations that involved planting of native C3 grasses in Canada successfully slowed invasion by *Agropyron cristatum*, an introduced C3 grass (Bakker and Wilson 2004). However, the results from my study suggest that attempts to control invasion of non-native species by manipulating functional groups may not be generally successful. In the field experiment, all non-native species which were added as seed did equally well across community types, and were approximately three times more successful at establishing than native species. Similarly, establishment and survival of non-native species in the mesocosm experiment was approximately five to ten times higher than native species. While non-native success in general differed among treatments in the mesocosm experiment, this was probably driven by just one of the four non-native species (*Centaurea maculosa*) that showed differences in affinity among the dominant treatments, having the lowest success in forb-dominated communities. It is possible that several years of competitive interactions will alter the relative success of these species (Levine et al. 2004), but my study shows very little effect of community composition on the initial establishment and survival of these invasive species.

Conclusions

The results from this study show that the identity of invaders is important to consider when examining factors contributing to the invasibility of communities. I did find differences in colonization success among different functional groups of invaders in both experiments, as well as between native and non-native invader species. Many studies of invasibility summarize invasion based on the establishment success of a single, often non-native, species (e.g., Robinson et al. 1995, Lyons and Schwartz 2001, Lindig-Cisneros and Zedler 2002, Smith et al. 2004). My results call into question the generality of results from such single-species addition studies. A community that is susceptible to invasion by one species, may be resistant to another species. Growing concern over the negative ecological and economic impacts of *exotic* species makes understanding what factors drive their invasion critical (Lonsdale 1999), while increased insight into the mechanisms of *native* species invasions is important for protecting and maintaining species diversity, successional dynamics, and community stability (Crawley 1987, Tilman 1997). Studies that add seeds of a variety of species may create undesired seedling competition effects, but they also give a more complete picture of how a community may respond to any given novel invader (e.g., Symstad 2000, Foster et al. 2002). Further, while mechanisms of limiting similarity would make success of invaders easier to predict, my study shows that such predictions are rarely upheld by experimental data. As ecologists search for generalities to explain ecological processes, it is important to acknowledge that dynamics of individual species are not always predictable.

CHAPTER 6

SUMMARY AND FUTURE DIRECTIONS

Summary

The work presented in this dissertation has addressed two stages of invasion: establishment and population spread. The restoration experiment in chapter two gives insight into our understanding of what regulates the growth and spread of populations of invasive species. It is important to understand dynamics of every life stage of a species in order to successfully predict effects of disturbance and management on long-term population growth. Population matrix modelling provides a more complete picture of effects of management on population responses, as compared with other measures based only on community composition or relative abundance. From a management perspective, it becomes important to consider the effects of conservation or restoration practices on noxious invasive species that may or may not have different life histories and responses to disturbance compared to native species.

The community studies presented in chapters three through five give insight into our understanding of what regulates the initial invasion process. I have shown that the identity of dominant species in communities can play as strong a role in regulating invasibility as community species richness, while the relative abundance of dominants seems to play only a small role. This knowledge may help managers and practitioners select effective species to use as dominants in restoration efforts to reduce or limit further invasions, or to use in native species seed additions to take advantage of highly invasible non-native communities (e.g., Seabloom et al. 2003, Suding et al. 2004). Further, I found that community species richness was actually positively related to invasibility in the field, suggesting that ecology still does not have a full understanding of how community diversity, in all its aspects, and invasibility are related.

Future Directions

My dissertation work addressed the relationship between community diversity and invasibility from a purely competition perspective. In fact, most studies of invasibility have assumed that competition, predation, and disturbance are of primary importance in regulating community dynamics (e.g. Hobbs and Huenneke 1992, Tilman 1997, Naeem et al. 2000, Davis and Pelsor 2001, Shea and Chesson 2002). Recently though, a few studies have suggested that mutualisms may be equally important in community invasibility. For example, the success of *Pinus* invasions in the southern hemisphere has been attributed to mutualisms with ectomycorrhizal fungi (Richardson et al. 2000). From a community perspective, recent research has shown that differences in mycorrhizal communities can have large impacts on seedling establishment in grasslands (e.g., Moora and Zobel 1998, van der Heijden 2004).

While my dissertation work has shown that dominant species play an important role in invasibility of communities, the mechanisms that cause this are still unclear. For post-doctoral work, I am interested in pursuing research that examines the relationships between dominant species, mutualists, and invasion. Specifically, I propose to examine two common and widespread plant mutualists, arbuscular mycorrhizal fungi (AMF) and endophytic fungi (EF) to address the question: Can microbial mutualists alter dominance and invasion in plant communities?

AMF are common plant associates and can strongly improve host plant performance. AMF are associated with 80% of all angiosperms and form symbioses with roots, where they exchange water and nutrients for carbon from the plant, helping the plant acquire needed resources in stressful environments (Smith and Read 1997). Although most AMF have been considered diffuse mutualists, different species of mycorrhizae are now known to vary in both host specificity and benefits to hosts (Bever 2003). For example, when inoculated with one of four different species of AMF, some plant species exhibited large variation in growth responses to different fungi, while others expressed consistent responses across all AMF species (van der Heijden et al. 1998a).

Several lines of evidence support a role for AMF in community invasibility. Prior studies have shown that the presence (or diversity) of AMF can increase native plant diversity and suggest that AMF facilitate community invasibility (e.g. Koske and Gemma 1997, Rosales et al. 1997, Smith et al. 1998, van der Heijden et al. 1998, Bever et al. 2003). For example, in a microcosm experiment using perennial grasses, AMF inoculations increased seedling establishment (van der Heijden 2004). In contrast, some studies have documented AMF-mediated reductions in invasibility when AMF promote the dominance of a single native species (e.g., Harnett and Wilson 1999). Furthermore, other studies show that AMF increase the success of non-native species, such *Centaurea maculosa* (spotted knapweed) in the western US, which can parasitize resources from native plants through AMF connections (Carey et al. 2004, Callaway et al. 2004), or *Solidago canadensis* (Canada goldenrod) in China where invasion success appears related to the abundance of particular AMF species (Jin et al. 2004). In a microcosm experiment, Stampe and Daehler (2003) showed that AMF diversity affected invasion success of the non-native *Bidens pilosa.* From this prior work, we can conclude that the identity of the community dominant, the invading plant, and the associated AMF are likely to be important factors in predicting how AMF affect community dynamics and invasion (Umbanhowar and McCann 2005). However, most studies of AMF-plant relationships are still limited to "coarse scale" (presence/absence) experiments on AMF using individual plants in the greenhouse, rather than whole plant communities (Hart et al. 2003). While such studies are informative, a fine-tuned understanding of AMF will require manipulations of AMF diversity and responses measured at the community, rather than individual, scale (Johnson et al. 1997).

Systemic EF are widespread in plants and can have strong effects on host performance. Systemic EF are specialized mutualists that grow in intercellular spaces of aboveground plant tissue and are estimated to form relationships with 20-30% of all grass species, especially with cool-season (C3) species in subfamily Pooideae (Saikkonen et al. 1998). In grass hosts, EF can increase drought tolerance and nutrient uptake (reviewed by Rudgers and Clay 2005), as well as resistance to herbivores through the production of bioactive, fungal alkaloids (reviewed by Clay and Schardl 2002). EF may have strong effects on plant competitive hierarchies, ecosystem processes, and community assembly, although these effects have largely been investigated in only a single system thus far. For example, in *Lolium arundinaceum*, prior work has shown that EF association increases competitive ability (Clay et al. 1993), reduces plant diversity (Clay and Holah 1999), reduces plant immigration and succession (Rudgers et al. unpub. data), and alters ecosystem properties, such as decomposition (Lemons et al. 2005). In other research, EF reduced microbial biomass and soil respiration by more than 80% (Franzluebbers et al. 1999), and increased soil organic carbon, nitrogen, and extractable phosphorus

(Franzluebbers et al. 1999; Schomberg et al. 2000). Alteration of these ecosystem processes may consequently affect invading species, but experiments are needed to test these proposed indirect mechanisms. EF may play important roles in plant invasions because they can strongly benefit host grasses, which constitute dominant members of many plant communities, including many non-native species. However, the effects of EF on community dynamics remain unresolved.

Further, plants can host several mutualists simultaneously, such as AMF and EF, and these may interact with each other through the shared partner, having community-level consequences (reviewed by Stanton 2003). For example, AMF can influence pollinator visitation by shifting allocation of plant resources toward shoots and reproductive structures, thereby increasing the number of pollinator visits (Wolfe et al. 2005). AMF and EF are known to interact strongly in *Lolium* species, including strong suppression of AMF abundance by EF mediated through the shared host plant (Guo et al. 1992, Chu-Chou et al. 1992, Muller 2003), interactive effects of EF and AMF on individual host plant fitness (Matthews and Clay 2001), and interactive effects on the abundance and performance of individual herbivores (Vicari et al. 2002). Although interactions between EF and AMF can clearly be strong, whether these interactions influence the associated plant community remains unresolved. For example, suppression of AMF by EF may reduce community invasibility if invading plants are highly dependent on AMF.

While there is definitely a need to examine the role of AMF and EF in the oldfield systems of my dissertation, there are logistical problems involved with AMF (e.g., it is almost impossible to address the role of AMF independent of other soil microbes, which are often radically altered in experiments that use fungicide to impose AMF treatments; Bayman et al. 2002) that make an alternative system a better choice. Sand dune plant communities provide unique opportunities to examine the role of microbial mutualisms as they are one of the few natural systems where plant and soil communities develop from initially sterile conditions. Both AMF (belowground) and EF (aboveground) form symbioses with plants that can help infected plants in stressful environments by increasing drought tolerance and nutrient uptake (Smith and Read 1997, Rudgers and Clay 2005), and so may have important impacts on dune invasion dynamics. Further, dune restorations provide ideal opportunities to study how changes in AMF and EF affect plant community structure, as restoration activities often alter microbial biota unintentionally. For future research, I am interested in using a combination of surveys and field and greenhouse experiments to address the following questions:

1. *Are AMF and EF more abundant in restored dunes than in natural dunes?*
2. *Are restored dunes more or less susceptible to exotic species invasion and native species colonization because of changes in these mutualists and their effects on the dominant species?*
3. *Do interactive effects of AMF and EF differ from their individual effects on community invasibility?*

To begin to explore these questions, I conducted a pilot survey of AMF and EF abundance in six dune communities of SW Michigan this past summer. This survey indicated that the diversity of AMF in natural dunes increased with distance from the lake, and the species composition of the natural dunes differed from that of a restored dune. Similarly, EF frequency (*Epichloë typhina)* in *Ammophila breviligulata*, the dominant native grass in most coastal dunes, differed between natural and restored sites, with the restored population having higher EF infection rates than the natural populations. A more extensive survey, taking advantage of protected natural dune communities and the history of active dune restoration projects by state and federal agencies throughout the Great Lakes region, will be an important first step at scaling effects of plant mutualisms to the community and landscape level.

Next steps involving manipulative experiments in the field and greenhouse will help elucidate mechanisms by which fungal mutualists may alter invasibility of communities. In the proposed study system, I expect that EF mutualists alone will reduce invasibility by increasing the competitive dominance of host plants (*Ammophila*), while AMF mutualists alone will increase invasibility by facilitating the establishment of subordinate, later-successional species as well as noxious, invasive species that have a higher dependence on the AMF mutualism. In addition, interactions between the two mutualists may yield effects on community structure not predictable from the study of pair-wise interactions alone (Stanton 2003). I expect that the presence of EF in *Ammophila* will suppress the effects of AMF on invasion.

Current evidence (Koske and Gemma 1997, Callaway et al. 2004, Rudgers et al. 2005) strongly suggests that fungal mutualists may be key to invasive species management. This proposed research will enhance understanding of how microbial mutualists contribute to dynamics of plant invasion, as well as directly bear on improving management of natural and restored dune communities.

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