

**Patterns and processes
of plant community invasibility**

by

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ABSTRACT

The invasion of native plant communities by exotic species is a cause for much environmental concern but also provides an opportunity to observe basic ecological processes. I quantified invasion rate in a series of experimental communities in order to test the hypothesis that lowered diversity leads to increased invasibility. The experiment was designed to provide a direct test of niche complementarity, the mechanism by which diverse communities are usually hypothesized to resist invasion. I also examined modes of invasion of one particular exotic species, crown vetch (*Coronilla varia* L.).

In the experimental communities I found that the relationship between diversity and invasibility varies depending on the attributes of community members. Lowering diversity by removing short species from big bluestem (*Andropogon gerardii* Vitman) dominated communities had no effect on invasibility. However, removing tall species from these communities did cause an increase in invasibility. This was contrary to expectations, as removing short species lowered the amount of height dissimilarity present in the communities, which would be expected to reduce niche complementarity and increase invasibility.

While we found no support for niche complementarity based on height dissimilarity, we found some support for niche complementarity through phenology. The vast majority of the invaders in our experimental prairie communities appeared in the spring and early summer. Communities that contained species that were actively growing and competitive at this time were better able to resist invasion. The practical implication of this result for prairie managers is that management regimes favoring warm season grasses may lead to reduced

resistance to invasion by cool season forbs and grasses, which make up a substantial portion of the weed flora in many prairie areas.

In the second part of my research I found that crown vetch patches have little spatial-age structure, possibly due to a rapid rate of ramet turnover. I also found that crown vetch does not build up a large presence in the seed bank of sites it has invaded, but that its ability to regenerate from vegetative fragments may be the key to its persistence.

CHAPTER 1. GENERAL INTRODUCTION

Two Views of Invasion

Elton (1958) is generally credited with having first brought widespread attention to the fact that human actions are causing many plant (and animal) species to rapidly expand their geographical ranges, and using the term “invasion” to describe the process by which species are transported outside of their native range and then spread in their new locations. The potential effects of these invasions have generated a great amount of environmental concern (Vitousek et al. 1996, Wilcove et al. 1998), as well as a great amount of debate about the extent to which this concern is warranted (Hager and McCoy 1998, Sagoff 2005). While determining the extent to which introduced plants actually cause ecosystem change (MacDougall and Turkington 2005) and understanding potential mechanisms by which they may do so (Davis 2003, Corbin and D’Antonio 2004) are certainly two of the major challenges facing ecologists today, there is also another way to look at plant introductions.

It is important to remember that plant communities have always been subject to change and that plant introductions have been happening for much longer than humans have been around to cause them. Certainly the number of introductions has increased recently due to human activity (Elton 1958), but at a fundamental level, there may be little difference between a species arriving at a new location through human actions and one arriving through natural dispersal (Vermeij 2005). Therefore, recent plant invasions give us an opportunity to study the kinds of biotic interactions that have always played a role in structuring plant communities (Bruno et al. 2005). The idea of looking at the behavior of introduced species to make inferences about fundamental biological principles is actually quite old. Charles

Darwin (1859) pointed to the rapid spread of some introduced plants as evidence that plant species are capable of developing disjunct ranges through natural spread in response to climatic or geologic change. While it is certainly reasonable to be concerned about the potential effects of introduced species on native ecosystems, we should also take advantage of the opportunity that introduced species offer us to learn about biotic interactions and community dynamics.

Diversity and Invasion

Understanding the factors that allow for species coexistence and govern diversity in plant communities is a central goal of community ecology (Morin 1999). One of the debates in this area is over the degree to which communities may become saturated as diversity increases (Stachowicz and Tilman 2005). One way to address this question is by studying the effects of diversity on the invasibility of communities. Elton (1958) first hypothesized that more diverse communities would have fewer available resources (be more saturated) than less diverse communities, and would therefore be less likely to be invaded. The mechanism by which a more diverse assemblage of species is hypothesized to efficiently take up resources, thus leaving fewer available to potential invaders, is now known as niche complementarity (e.g. Knops et al. 1999, Naeem et al. 2000, Kennedy et al. 2002). Classic ecological theory, which proposes a strong positive relationship between stability and diversity (MacArthur 1955, 1970), has long been seen as supporting Elton's hypothesis. However, tests of the hypothesis have produced mixed results. Landscape-scale studies have found a positive correlation between native and exotic species richness (Lonsdale 1999, Stohlgren et al. 2003, Brown and Peet 2003). However, it is not clear that a community with

high exotic species richness is necessarily a community that has been severely invaded or negatively impacted, especially when native species richness is also high. Cleland et al. (2004) found a positive correlation between native and exotic richness, but also found a negative correlation between native richness and exotic abundance, which is a more direct measure of invasion. Several experiments at the neighborhood scale appear to show that more species rich plots are better able to resist invasion (Tilman 1997, Knops et al. 1999, Hector et al. 2001, Kennedy et al. 2002), - but see Lavorel et al. (1999). Results from the neighborhood scale experimental studies have been seen as conflicting with those from the landscape-scale observational studies (Levine and D'Antonio 1999, Tilman 2004). However, this perceived conflict may simply be the result of factors that impact invasion, such as biotic resistance and propagule pressure, acting at different scales (Levine 2000).

Questions about the relationship between diversity and invasibility relate to some of the central issues in community ecology about community assembly, structure and function. Therefore, much research has already focused on this relationship, yet many questions remain unanswered and it remains an area of active interest. Several experimental studies have examined the relationship between diversity and invasibility (e.g. Tilman 1997, Kennedy et al. 2002), but ecologists have not come to any general agreement on how these studies should be interpreted (e.g. Crawley 1999, Wardle 2001) or whether they have been relevant to natural systems (Zavaleta 2004). Additionally, all research that focuses on relationships between diversity and ecosystem functioning has become more important as we realize the extent to which global biodiversity is declining (Chapin et al. 2000).

Objectives

The first objective of this research was to experimentally test the hypothesis that more diverse communities are more resistant to invasion than less diverse communities at the neighborhood scale. Unlike nearly all other studies that have examined this relationship, our experiment manipulated diversity in a realistic manner based on previously published studies of the experimental system (tallgrass prairie). Additionally, the experiment was designed in a manner that allowed for a direct test of the mechanism of niche complementarity, by which more diverse communities are hypothesized to better resist invasion.

The second objective of this research was initially to examine patterns of invasion by a specific invader, crown vetch (*Coronilla varia* L.), in relation to other vegetation at the sites being invaded in order to further investigate the effects of plant community dynamics on invasion success. However, it soon became clear that patterns in crown vetch invasion would be more difficult to characterize than was originally thought, and the focus of the research turned to examining the modes of spread and persistence of crown vetch.

Thesis Organization

The thesis is divided into four chapters. The first chapter gives general background information related to the study questions and places them into a general context. It also discusses the main objectives of the research. The second and third chapters are articles prepared for publication, both of which will be submitted to international journals. The final chapter discusses general conclusions that can be drawn from the research.

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CHAPTER 2. DIVERSITY-INVASIBILITY RELATIONSHIPS DIFFER BETWEEN TWO EXTINCTION SCENARIOS IN TALLGRASS PRAIRIE

A paper to be submitted to an international journal

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Abstract

Experiments that have manipulated species richness with random draws of species from a larger species pool have usually found that invasibility declines as richness increases. These results have usually been attributed to niche complementarity, and interpreted to mean that communities will become less resistant to invaders as species go locally extinct. However, it is not clear how relevant these studies are to real-world situations where species extinctions are non-random, and where species diversity declines due to increased rarity (i.e. reduced evenness) without having local extinctions. We experimentally varied species richness from 1 to 4, and evenness from 0.44 to 0.97 with two different extinction scenarios in plantings in western Iowa. In both scenarios, evenness was varied by changing the level of dominance of the tall grass *Andropogon gerardii*. In one scenario, which simulated a loss of short species from *Andropogon* communities, we directly tested for complementarity in light capture due to having species in mixtures with dissimilar heights. We contrasted this scenario with a second set of mixtures that contained all tall species. In both cases, we controlled for factors such as rooting depth and planting density. Mean invader biomass was higher in monocultures (121 g/m²/week) than in 4-species mixtures (49 g/m²/week). Reduced evenness due to increasing *Andropogon* dominance did not affect invader biomass in mixtures with

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dissimilar heights. However, the amount of invader biomass did decrease significantly as evenness increased across mixtures with all tall species. These results suggest that the effect of reduced species diversity on invasibility are 1) not related to complementarity through height dissimilarity, and 2) variable depending on the traits of the species that are becoming rare or going locally extinct.

Introduction

Several neighborhood scale experiments have found that increased species richness increases invasion resistance (Tilman 1997, Knops et al. 1999, Hector et al. 2001, Kennedy et al. 2002)—but see Lavorel et al. (1999). However, the interpretation of these experiments and their relevance to real-world situations have been questioned (e.g. Lonsdale 1999, Crawley 1999, Wardle 2001, Stohlgren et al. 2003, Brown and Peet 2003, Zavaleta 2004). One interpretation is that the greater resistance to invasion observed in more diverse plots results from niche complementarity (e.g. Knops et al. 1999, Naeem et al. 2000, Kennedy et al. 2002). Plots with more species are said to more efficiently utilize resources such as light and nutrients, leaving fewer potential opportunities for invaders. In contrast, Crawley et al. (1999) and Wardle (2001) have argued that the observed pattern is actually the result of the sampling effect, or the greater likelihood of more diverse plots containing one of the few aggressive species that actually drive a community's ability to resist invasion. It is now generally accepted that these interpretations are not mutually exclusive, as both niche complementarity and the sampling effect could be acting at the same time (Hooper et al. 2005).

Another question about the interpretation of these experiments arises from the use of species richness as a surrogate for diversity (Stirling and Wilsey 2001). Richness alone does not completely account for the diversity of a system, as it does not include relative abundance or rarity and in many cases is only weakly correlated with them (Stirling and Wilsey 2001, Wilsey et al. 2005). Diversity has both richness and evenness components. However, very few studies of diversity and invasibility have considered evenness, dominance or other measures that incorporate relative abundance. In one of the few studies that has manipulated evenness, Wilsey and Polley (2002) used four grassland species and found that plots with higher evenness tended to be less invaded. Additionally, Smith et al. (2004) found that invasibility increased with dominance by warm season grasses, and that there was no relationship between invasibility and richness. Examining the effects of evenness upon invasibility may be more directly applicable to natural systems than studies that look at richness alone, because species often become rare but not extinct (Wilsey and Potvin 2000, Chapin et al. 2000). Manipulating evenness as opposed to richness also has the benefit of removing the sampling effect because diversity can be changed while still including the same species in mixtures (Wilsey and Potvin 2000, Loreau et al. 2001, Wilsey and Polley 2002). Additionally, relative abundance may be more directly influenced by species interactions than richness, which may be driven more by immigration and emigration (Stirling and Wilsey 2001).

Kennedy (2002) and others have argued that the increased resistance to invasion observed with increasing species richness in experimental plots means that natural systems will become more invaseable as species become extinct (i.e. richness declines). However, the relevance of many neighborhood-scale studies of diversity and invasibility to natural systems

can be questioned on the grounds that species richness in the experiments is usually manipulated by planting plots with differing numbers of species randomly selected from a species pool. Therefore, these studies are only directly relevant to situations where species are randomly going extinct (Zavaleta 2004, Bunker et al. 2005). It is not clear if results from such experiments are applicable to natural systems, as extinctions are unlikely to be random events (Leach and Givnish 1996, Fischer and Stocklin 1997, Wardle 1999, Duncan and Young 2000, Chapin et al. 2000, Wilsey and Polley 2004, Zavaleta 2004). Leach and Givnish (1996) found that short forbs and legumes went locally extinct more frequently than tall and non-leguminous forbs in small isolated prairie remnants in Wisconsin. Current grassland management practices also tend to favor tall warm season grasses over forbs and cool season grasses (Collins et al. 1998, Martin et al. 2005), which leads to low diversity grasslands with many forbs being extremely rare. Lyons and Schwartz (2001) removed rare species from grassland plots in California and found that this increased the ability of the invader *Lolium multiflorum* Lam. to establish when it was seeded into the plots. In another California grassland experiment, Zavaleta (2004) manipulated grassland species richness in a manner designed to mimic changes observed in long-term data. When the invader *Centaurea solstitialis* L. was seeded in to the plots, increased species richness reduced *Centaurea* biomass much more than had been predicted based on previous trials that manipulated richness levels with random species losses. Recent modeling work has also shown that different extinction scenarios can be expected to have dramatically divergent effects on ecosystem processes (Bunker et al. 2005). Therefore, in order to understand the relationship between diversity and invasibility, as it might exist in a natural setting, it is necessary to design experiments that move beyond random manipulations and consider more ecologically

realistic extinction and rarity scenarios (Zavaleta 2004). A more ecologically realistic approach to biodiversity-ecosystem function research has been advocated as a means to make the results of basic ecological research more relevant to conservation (Schwartz 2000, Srivastava and Vellend 2005).

Our study used experimental plots to test the hypothesis that increased diversity leads to increased resistance to invasion at the neighborhood scale due to greater niche complementarity. We experimentally manipulated species evenness within mixtures in a manner designed to mimic two rarity/extinction scenarios known to occur in prairies. In one scenario, short species become rare and then are lost from *Andropogon gerardii* Vitman dominated communities, as has been observed in small isolated remnant prairies (Leach and Givnish 1996). This may have impacts on invasibility due to a reduction in species dissimilarity. Greater dissimilarity in height can be related to net primary productivity (Naeem et al. 1994, Wilsey and Potvin 2000). By varying dissimilarity in height, we were able to directly test, for the first time, the role of niche complementarity in determining the degree of resistance to invasion. Previous tests have been indirect in that they vary functional group number and composition (Loreau et al. 2001). In the second scenario, only tall species were included in the mixture, and tall subordinate species abundance was reduced as *Andropogon gerardii* increased in dominance across treatments. This follows a pattern often observed in prairies, where management (e.g., frequent spring fire) can cause one or a few tall warm season grasses to become extremely dominant (Collins et al. 1998, Howe 2000, Martin et al. 2005).

In both scenarios, forbs decreased in abundance with increased grass dominance, which is known to happen in many prairies under management regimes with frequent spring

fires and no grazing (Towne and Owensby 1984, Collins et al. 1998, Howe 2000). Both scenarios were designed so that big bluestem (*Andropogon gerardii* Vitman) became more dominant as evenness decreased. This is ecologically realistic, as *Andropogon* is often a dominant species in tallgrass prairies, and it has been observed to become especially dominant in reconstructed prairies (Sluis 1999, Martin et al. 2005). The evenness levels used bracketed the differences typically observed between restored prairies, which generally have low evenness and high dominance by C4 grasses, and remnant prairies, which tend to have a more even mix of grasses and forbs (Martin et al. 2005).

We predicted that plots with higher diversity, either richness (monocultures versus mixtures) or evenness, would be less invaded than plots with lower diversity. We also predicted, due to greater niche complementarity, that plots containing more height dissimilarity (i.e., those plots with both tall and short species present) would be less invaded than plots containing more similar heights among species.

Methods

Study Site and Species Used

The experiment was conducted on a hill in an abandoned pasture at Iowa State University's Western Research Farm, which is located in Monona County in the loess hills region of Iowa. The pasture had not been grazed for several years and had not been fertilized in at least a decade. The dominant species in the pasture prior to the establishment of our plots was smooth brome (*Bromus inermis* Leyss.).

We used six species native to the loess hills in our plots: the tall, deeply rooting warm season grass *Andropogon gerardii* Vitman and the tall, shallowly rooting, warm season grass

Schizachyrium scoparius (Michx.) Nash, the short, shallowly rooting warm season grass *Bouteloua gracilis* (H.B.K.) Lag. ex. Griffiths, the tall, shallowly rooting forb *Heterotheca villosa* (Pursh) Shinnars, the tall, deeply rooting forb *Salvia azurea* Lam., and the short, shallowly rooting forb *Liatris punctata* Hook. Published heights and rooting depths were available for all of these species (Sun et al. 1997, Craine et al. 2002) (Table 1). It was especially important to control rooting depth so that height dissimilarity could be tested without this confounding variable. Thus, we were limited to species with published rooting depths. We verified that species we considered tall were actually taller than our short species by measuring the heights of at least 3 plants in each plot in August of each sampling year (Table 1).

Experimental Plots

All plots were 1 m² and were established at a density of 72 plants/m². This density was chosen based on average densities that we sampled in a nearby loess hills prairie remnant (42.10° N, 95.97° W). We surveyed eight 1m² plots 1.5 months after a spring fire, when individuals could be differentiated, and found an average density of 68.5 plants/m² (range of 45-94).

All plots were established with small, equal-size transplants. A random sample of plants at the time of planting in 2003 averaged 0.6 g/plant and did not vary among species ($F_{5,30}=1.7$ $p=0.17$). All transplants were grown in potting soil in 4-inch pots, with several plants per pot, in an ISU greenhouse. Once planted in the field, the transplants were watered once to facilitate survival, but remained un-watered thereafter. The plots were kept weeded and allowed to establish for one growing season, with data collection beginning in the second season.

Each of the six species used was planted in monoculture plots. Our two rarity/extinction scenarios were set up in two sets of mixture plots (Table 1). One set of mixtures contained all tall species (T-plots), and the other set contained both tall and short species (D-, or dissimilar plots). Species richness (4) was constant across all these plots, but there were high, medium and low evenness treatments. T-plots contained *Andropogon*, *Salvia*, *Schizachyrium*, and *Heterotheca*. D-plots contained the tall species *Andropogon* and *Salvia*, and the short species *Bouteloua*, and *Liatris* (Table 1.).

Evenness Treatments

Species evenness of mixtures was varied by planting species with relative abundances in a way that would change the slope of species rank-abundance relationships (Figure 1; Wilsey and Polley 2004). Rank-abundance slopes are often used as a diversity measure that encompasses both richness and evenness (Tokeshi 1993), but when species richness is held constant, as it was in our mixtures, slopes of rank-abundance relationships measure evenness alone. Our D-plots were planted so that the short species *Bouteloua* and *Liatris* decreased in abundance as evenness declined. In T-plots *Heterotheca* and *Schizachyrium* decreased in abundance as evenness declined. In both T and D-plots *Andropogon* abundance increased as evenness declined (Table 1).

We chose the slopes of the rank abundance relationships used in our plots based on an analysis of data from Martin et al. (2005) (Table 2.). Our treatments bracketed the observed differences between restored and remnant prairies, with the observed rank-abundance slopes in restored prairie falling between our low and medium evenness plots and the observed values in remnants falling between our medium and high evenness plots (Figure 1 and Table 2).

Trial and Block Design

The experiment was conducted in two separate trials, with 36 plots per trial. Each trial consisted of three complete blocks, one each on the North, East and Southwest slopes of the hill where the experiment took place. Each block contained each evenness treatment of both sets of mixtures, as well as each species in monoculture, for a total of twelve plots per block. The first trial was planted in 2003, with data collection beginning in 2004, and the second trial was planted in 2004 with data collection in 2005.

Invasion Rate

Invasion rate was quantified by sampling plants that recruited into the plots as volunteers. In this study system, volunteers mainly consist of exotic species and cosmopolitan weeds. Sampling the natural recruitment of these plants was a more realistic estimate of invasion than sampling one or a few planted species. All volunteer plants were removed in mid-April, early June, early July and mid-October of both sampling years, sorted by species, dried and weighed. These weeding dates were chosen during the first trial by observing the plots and weeding as needed, in order to remove weed seedlings with minimal disturbance of the soil surface. The amount of biomass removed from each plot was divided by the number of weeks since the previous weeding to obtain a rate ($\text{g/m}^2/\text{week}$) of species invasion for each plot. In the case of the April weeding, the amount of biomass removed was divided by the number of weeks since March 1, which was approximately the date of spring green up at the site in both years of the experiment.

We separated total invader biomass by taxon into grasses, forbs and legumes in order to test the hypothesis that treatments will differentially affect different taxa, and to examine

the question of whether diversity-invasibility relationships are generalizable or taxon specific.

Light

We measured the proportion of photosynthetically active radiation (PAR) reaching ground level in each plot with a Decagon Accupar light meter in June, July and September of both sampling years (Figure 4). Because our weeding dates were timed to prevent invaders from becoming very large, measuring the amount of light at ground level was an accurate method of determining light capture by the planted canopy. We compared trends in invasion rate data to light data in order to see if canopy light penetration was correlated with invasion rate.

Monoculture Comparisons

We compared invasion rates and light levels among monocultures in order to look for potential species effects caused by individual species being particularly vulnerable or resistant to invasion.

Seeded Invader

In the first three blocks, those established beginning in 2003, forty-nine *Coronilla varia* L. seeds were planted, in a 7x7 grid pattern, in each plot on April 14, 2004. Seedling emergence was monitored through June 15, 2004, at which time all but two of the seedlings in each plot were removed. Two small *Coronilla* transplants were also added to each plot on June 15. Survival and growth of all *Coronilla* plants was monitored throughout the 2004 growing season and spring of 2005. This procedure was not repeated in 2005 due to low rates of seedling and transplant growth and survival.

Statistical Analyses

We used SAS repeated measures ANOVA to test for treatment differences in invasion rate and the proportion of light reaching the soil surface over the course of the growing season. Invasion rate data were ln-transformed due to non-constant variance. When invasion rate data were broken into separate taxa we did not include either the April or October weeding dates in the analyses because too many plots were not invaded by all taxa at these dates, leaving too many zeroes in the data set (Figure 3).

A set of seven *a priori* linear contrasts were used to test for differences among treatments in both the light and invasion rate data sets. These contrasts were as follows: (1) The mean of all monoculture plots was compared to the mean of all mixtures based on the hypothesis that increased species richness would lead to lower rates of invasion in mixtures; (2) T-plots were compared to D-plots to test the hypothesis that the greater dissimilarity in height present in D-plots would lead to lower rates of invasion and light penetration through niche complementarity; (3) The effect of evenness treatments was tested across all mixtures to test the general hypothesis that increased evenness would lead to lower rates of invasion. The effect of evenness treatments was tested in (4) T-plots alone and (5) D-plots alone in order to determine the effect of evenness in each specific rarity/extinction scenario and see if these effects differed from the general trend tested in contrast #3. The effect of *Andropogon* dominance was tested in (6) T-plots and (7) D-plots in contrasts that included the *Andropogon* monocultures to test the hypothesis that increased warm season grass dominance would lead to greater invasion (Smith et al. 2004).

All contrast coefficients were based on planted rank-abundance slopes and *Andropogon* dominance and calculated using PROC IML (SAS Institute). In evenness

contrasts the coefficient values were 0.73, -0.06, and -0.68 for H, M and L plots. In *Andropogon* dominance contrasts the coefficient values were 0.71 in the *Andropogon* monocultures and 0.16, -0.21 and -0.65 in the L, M, and H plots. All plots were inventoried during June of the year they were sampled, and observed rank abundance relationships and *Andropogon* dominance did not differ significantly from the planted levels. With each *a priori* linear contrast we tested for lack of fit by adding a quadratic term (Petersen 1985), and then removed it if lack of fit was not significant. This was necessary in order to detect any possible non-linear relationships in the data, as these would not be found with linear contrasts alone. All analyses used type IV sums of squares because one *Liatris* monoculture was not planted during the first trial due to a shortage of transplants and this caused a missing cell.

All comparisons among monocultures were made using Tukey-adjusted comparisons of least squares means.

Results

Invasion rate

The mean rate of invasion was higher in monocultures (121 g/m²/week) than in mixtures (49 g/m²/week) (Table 3 and Fig. 2). The magnitude of the difference between monocultures and mixtures varied across time ($F_{3,168}=3.27$, $p=0.02$), but the mean rate of invasion for monocultures was always higher than for mixtures and this difference was significant for all weeding dates except April (Fig. 2). Invasion rate was not consistent throughout the growing season. In both years, there was a much greater biomass of invaders between April and July than either earlier or later in the growing season (Fig. 2. Table 3, Time main effect $p<0.001$).

Interestingly, and contrary to our hypotheses, there was no significant effect of overall evenness on invasion rate in mixtures (Table 3) and the effect of evenness was actually less important in plots with dissimilar heights (Table 3). There was no overall difference in invasion rate between T and D -plots (Table 3). We had hypothesized that D-plots would be less invaded due to niche complementarity resulting from the inclusion of both tall and short species in these mixtures, but found no support for this hypothesis. In the D-plots, where the abundance of short species decreased and *Andropogon* increased as evenness declined, there was no relationship between evenness and invasion rate (Table 3). However, in the T-plots there was a significant, negative linear relationship between invasion rate and evenness (Table 3, Fig. 2).

Taking into account *Andropogon* monocultures and testing for dominance effects yielded results consistent with those for evenness effects in mixtures (Table 3, Fig. 2). Linear contrasts that included the *Andropogon* monocultures and compared *Andropogon* dominance to invasion rate were not significant in the D plots, but showed a significant, linear decrease in invasion rate in the T plots as *Andropogon* dominance decreased (i.e. evenness increased) (Fig. 2). Although the direction of this relationship was the same in all months, the contrast had a significant interaction with time ($F_{3,168} = 3.7, p = 0.013$). It was steeper and significant in April and June ($F_{1,56} = 6.61, p = 0.0128$ and $F_{1,56} = 11.93, p = 0.001$) and became more shallow and lost significance in July and October ($F_{1,56} = 3.82, p = 0.056$ and $F_{1,56} = 0.67, p = 0.42$). None of the quadratic contrast terms added to test for lack of fit were significant.

The invader biomass consisted of exotic species and cosmopolitan weeds. Breaking down invader biomass by taxon and analyzing grasses, non-leguminous forbs and legumes separately showed that treatment effects observed in the total biomass analysis were driven

by the responses of grasses and forbs. The legumes recruiting into our plots, mainly *Medicago lupulina* L. and *Trifolium pratense* L, were not significantly affected by our experimental treatments (Table 3, Fig. 3). Grasses, including *Bromus inermis*, *Poa* spp. L., and *Setaria* spp Beauv., and forbs, such as *Conyza canadensis* (L.) Cronq., *Cirsium* spp. P. Mill., *Taraxacum officinale* Weber, *Chenopodium album* L., *Ambrosia* spp. L. and *Verbena* spp. L., generally followed the same trends as total invader biomass data (Table 3, Fig 3.)

In the analysis of grass biomass, one of the quadratic terms added to linear contrasts to test for lack of fit was significant. Adding a quadratic term made the contrast for the effect of *Andropogon* dominance in D plots significant ($F_{1,56}=4.5$, $p=0.04$). This contrast was not significant without the quadratic term (Table 3), suggesting that grass invasion initially declined with *Andropogon* dominance in D plots but then increased as *Andropogon* dominance decreased further (Fig 3).

Seeded Invader

There were no differences among plots in *Coronilla* seedling emergence ($F_{13,21}=1.25$, $p=0.31$). After the seedlings were thinned to two per plot and the two transplants were added, *Coronilla* growth was uniformly poor. Of the over 5,500 grams of invader biomass harvested from the 2004 trial, less than 150 grams were *Coronilla*. The poor growth of *Coronilla* throughout the 2004 trial made it impossible to determine the presence or absence of any treatment effects upon this seeded invader. It is highly unlikely that adding *Coronilla* to one trial and not the other confounded our other results in any way, as there was so little *Coronilla* growth and all statistical analyses treated trial as a block term.

Light

Proportion of light reaching the soil surface followed trends similar to those seen in the invasion rate data (figure 4). The mean amount of light reaching the ground over the growing season was significantly higher in monocultures (34.5% of PAR) than in mixtures (15.1%). This contrast had a significant interaction with time ($F_{2,112}=5.76$, $p=0.004$), but was significant at all sampling dates and did not change direction. There was no significant relationship between evenness and light penetration, either overall or within the T or D plots. Surprisingly, given the presence of short species in D plots, there was no significant difference in the amount of light reaching the ground surface between T and D plots (Table 3). The effect of *Andropogon* dominance upon light penetration was significant in the T plots (Table 3). This contrast had a significant interaction with time ($F_{2,112} = 3.89$ $p=0.02$). As was the case with the relationship between invasion rate and *Andropogon* dominance in the T-plots, light penetration increased with *Andropogon* dominance earlier in the growing season (June $F_{1,56}=6.34$ $p=0.015$), but there was no significant relationship later on (July $F_{1,56} =2.18$ $p=0.15$, September $F_{1,56}=1.35$ $p=0.25$).

Monocultures

Liatris plots had both the greatest amount of light penetration and highest rate of invasion at all sampling dates (Figures 2 and 4). *Heterotheca* generally had the lowest rate of invasion and least light penetration (Figures 2 and 4). Early in the growing season, when there was a positive, linear relationship between both light penetration (June $F_{1,56} = 6.34$, $p=0.015$) and invasion rate (June $F_{1,56} = 6.61$, $p= 0.001$) and *Andropogon* dominance in the T-plots, *Heterotheca* monocultures had less than half the mean amount of canopy light penetration of *Andropogon* monocultures (21% versus 43%) and also had a significantly

lower rate of invasion (Tukey adjusted comparison $\alpha < 0.05$). The differences in light penetration and invasion rate between *Andropogon* and *Heterotheca* monocultures became insignificant later in the growing season, as did the effects of *Andropogon* dominance in the T-plots.

Discussion

We used two ecologically realistic rarity/extinction scenarios to experimentally test the hypothesis that less diverse plant communities are easier to invade than more diverse communities at the plant neighborhood scale. We found that changing rank-abundance relationships in *Andropogon gerardii* dominated communities by decreasing the abundance of short species, as has been documented to occur in small, isolated remnant prairies (Leach and Givnish 1996), had no significant effect on invasibility. However, lowering the abundance of other tall species in *Andropogon gerardii* dominated communities, which is frequently the observed difference between remnant and restored prairies (Martin et al. 2005), led to a linear increase in invasibility (Table 2, Figure 1). This may have been caused, at least in part, by the effect of decreased canopy light capture, which was correlated with decreased *Andropogon* dominance and increased abundance of other tall species. These results suggest that the effects of increased rarity and extinction on the invasibility of plant communities will vary greatly depending upon which species are becoming rare or going extinct, and supports modeling work by Bunker et al. (2005) showing highly variable effects of different extinction scenarios upon ecosystem functioning.

When we broke down the invader biomass by taxon, we found that different taxa responded differently to our treatments. Grasses and non-leguminous forbs responded

similarly and drove the trends seen in the total biomass data, but legumes were not significantly different. If we had only collected data on legumes that invaded our plots, we would have incorrectly concluded that our treatments had no effect on invasion. This supports the conclusion of Wilsey and Polley (2002), that it may be inappropriate to make general statements about the invasibility or resistance of a community based on experiments that use only one or a few seeded invaders.

The mechanism by which diversity is most often hypothesized to influence invasibility is niche complementarity—a more diverse assemblage of species is thought to be better able to monopolize available resources and exclude invaders than a less diverse assemblage (Knops et al 1999, Hector et al. 2001, Kennedy et al. 2002). If this mechanism is working, it should be possible to quantify and describe functional diversity more accurately than just by species number (Symstad 2000). A four species assemblage in which all four species are highly similar to one another should be easier to invade than a four species mixture containing more dissimilar species. In this experiment we controlled for rooting depth and taxonomic group, but varied height. This was the first direct test of the effect of species dissimilarity on invasion, because tests using functional group are number are only indirect (Loreau et al. 2001). We chose to vary height because greater dissimilarity in height can be related to net primary productivity (Naeem et al. 1994, Wilsey and Potvin 2000). We hypothesized that niche complementarity would cause mixtures containing both tall and short species to be less invaded than mixtures containing only tall species, but found no support for this hypothesis. However, within the tall species mixtures we did find some evidence of niche complementarity based on phenology. Differences across time periods had important effects in our experiment. We found heavy invasion pressure from mid-spring to early

summer, with many fewer invaders appearing in any plots either very early in the growing season or from mid-summer on. Monocultures of *Heterotheca*, a cool season forb that begins using resources early in the spring, were more resistant to invasion than monocultures of *Andropogon*, a warm season grass. In our tall plots, invasion resistance increased as *Andropogon* dominance declined and *Heterotheca* abundance increased. This may have been driven by *Heterotheca*'s ability to capture light early in the growing season, when invasion pressure was heaviest. Other studies of diversity effects on ecosystem processes have found phenology to be as or more important than other measures of functional similarity (Hooper and Vitousek 1997, Hooper 1998). This has not usually been addressed in studies of the diversity-invasibility relationship. However, authors of these studies have usually reported only seasonal totals for invaders, commonly sampling only once during the growing season (e.g., Symstad 2000), perhaps on the implicit assumption that invasion pressures will be more or less consistent over the course of a growing season. In our system at least, this was not the case. In one experiment that did consider phenology, Zavaleta (2004) found that more diverse communities were more likely to contain species that competed for resources later in the growing season. These communities were better at resisting invasion by star thistle (*Centaurea solstitialis* L.) because more members of these communities were actively using resources at the same time as this seeded invader.

Our results have practical implications for managing prairies. We included all volunteers appearing in our plots as invaders in our study, and found the great majority of them to appear in the spring and early summer. This suggests that another negative effect of overly frequent fires, or other management regimes that favor warm season grasses, beyond loss of diversity (Townes and Owensby 1984, Collins et al. 1998, Martin 2005), may be

reduced resistance to invasion by cool season forbs and grasses, which make up a substantial portion of the weed flora.

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Table 1. Composition of experimental plots in a planted field experiment in Western Iowa. The height column shows the measured mean height (cm) reached by each species in the experiment. The number in parentheses is the standard deviation of the measured mean. The rooting depth columns gives the classification, deep or shallow, of each species' rooting depth. Sources for these classifications are given below.

Plot type	All Tall					Dissimilar Heights			<i>Andropogon</i>
	Height	Rooting depth	High	Medium	Low	High	Medium	Low	Monoculture
<i>Andropogon</i>	133.2 (18.0)	deep ¹	22	38	52	22	38	52	72
<i>Salvia</i>	94.5 (17.3)	deep ²	19	19	15	19	19	15	
<i>Bouteloua</i>	44.6 (8.8)	shallow ^{1,2}			17	10	4		
<i>Liatris</i>	42.0 (10.5)	shallow ²			14	5	1		
<i>Schizachyrium</i>	84.1 (14.8)	shallow ^{1,2}	17	10	4				
<i>Heterotheca</i>	96.9 (12.0)	shallow ²	14	5	1				
Dominance ³			0.31	0.53	0.72	0.31	0.53	0.72	1
Evenness ⁴			0.97	0.67	0.44	0.97	0.67	0.44	undefined

¹ Craine et al. 2002

² Sun et al. 1997

³ Dominance by *Andropogon*

⁴ Simpson's evenness $(1/\sum p_i^2)/S$

Table 2. Mean slopes (SE) and ANOVA results for rank-abundance (\log_{10} [relative biomass] \times species rank) relationships among three remnant (Morris, Rolling Thunder, Sheeder) and one restored tallgrass prairie (Neal Smith National Wildlife Refuge) in southern Iowa. Letters denote differences (a priori contrasts, $P < 0.001$) between the three remnants ($n = 8$ per remnant) and the restoration ($n = 8$) within dates. See Martin et al. (2005) for sampling methods.

Sampling time	Morris	Rolling	Sheeder	Neal Smith
June 2003	- 0.14 ^a	- 0.18 ^a	- 0.17 ^a	- 0.33 ^b
August 2003	- 0.16 ^a	- 0.22 ^a	- 0.18 ^a	- 0.41 ^b

Table 3. Results From ANOVAs of invader biomass and canopy light penetration as a function of planted species evenness and richness in a field experiment in Iowa. Total biomass shows analysis of all invader biomass over all weeding dates, while the other columns separate this biomass by taxon and include only the June and July weeding dates. In the a priori contrasts, *Andropogon* dominance T and *Andropogon* dominance D include the *Andropogon* monocultures and only the tall (T) or dissimilar (D) plots.

Source	d.f.	Biomass F	Grasses F	Forbs F	Legumes F	Light F
Year	1	17.7 ***	157.6 ***	29.62 ***	134.9 ***	4.7 *
Block	2	15.3 ***	0.4	9.6 ***	24.7 ***	0.01
Plot	11	4.4 ***	7.1 ***	3.83 ***	1.3	13.8 ***
a priori linear contrasts						
monocultures vs. mixtures	1	7.7 **	12.2 ***	5.29 *	2.3	57.3 ***
Dissimilar (D) vs Tall (T) plots	1	1.6	3.6	0.55	1.1	0.9
overall evenness	1	0.8	0.3	0.25	0.5	0.04
evenness within T plots	1	4.05 *	4.05 *	1.08	1.13	0.4
evenness within D plots	1	0.57	1.4	0.11	0.01	0.1
<i>Andropogon</i> dominance (T)	1	8.2 **	10.6 **	3.17	3.8	4.5 *
<i>Andropogon</i> dominance (D)	1	0.3	0.1	0.3	0.5	0.9
error	56					
Time	3	381.1 ***	35 ***	25.2 ***	2.4	67.8 ***
Time X Year	3	30.9 ***	3.4 +	7.3 **	3.9	5.5 **
Time X Block	6	5.8 ***	1.7	1.6	5.8 *	2.9 *
Time X Plot	33	1.8 **	2.7 **	1.5	1.2	5.6 ***
error	168					

* = p < 0.05

** = p < 0.01

*** = p < 0.001

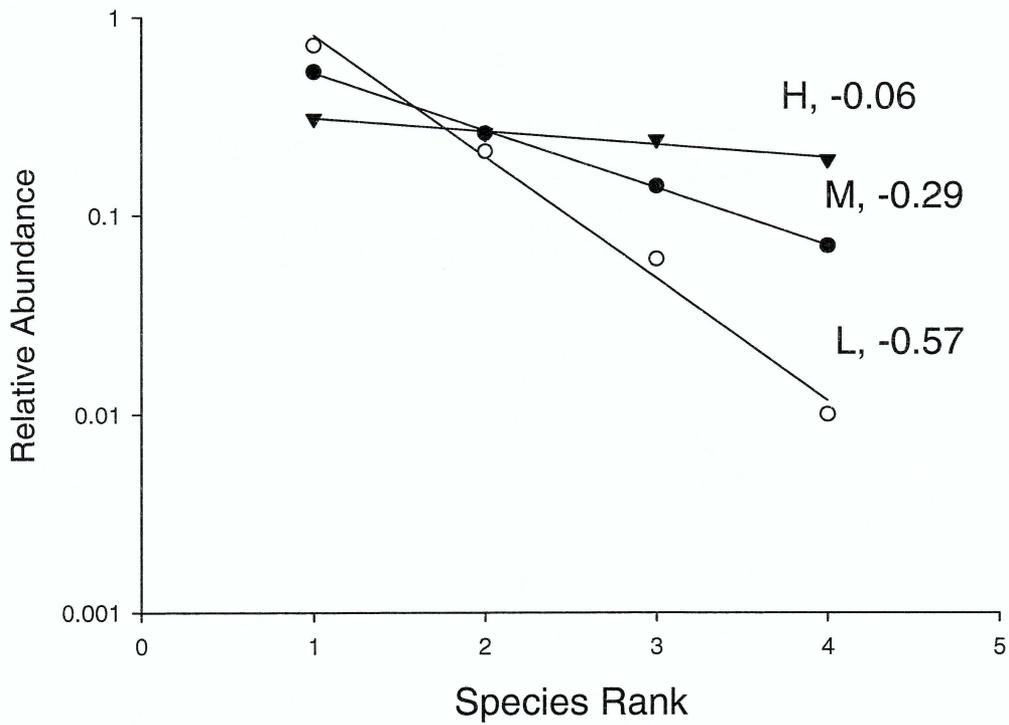


Figure 1. Planted log rank-relative abundance slopes in the high (H), medium (M), and low (L) evenness treatments in a field experiment in Western Iowa.

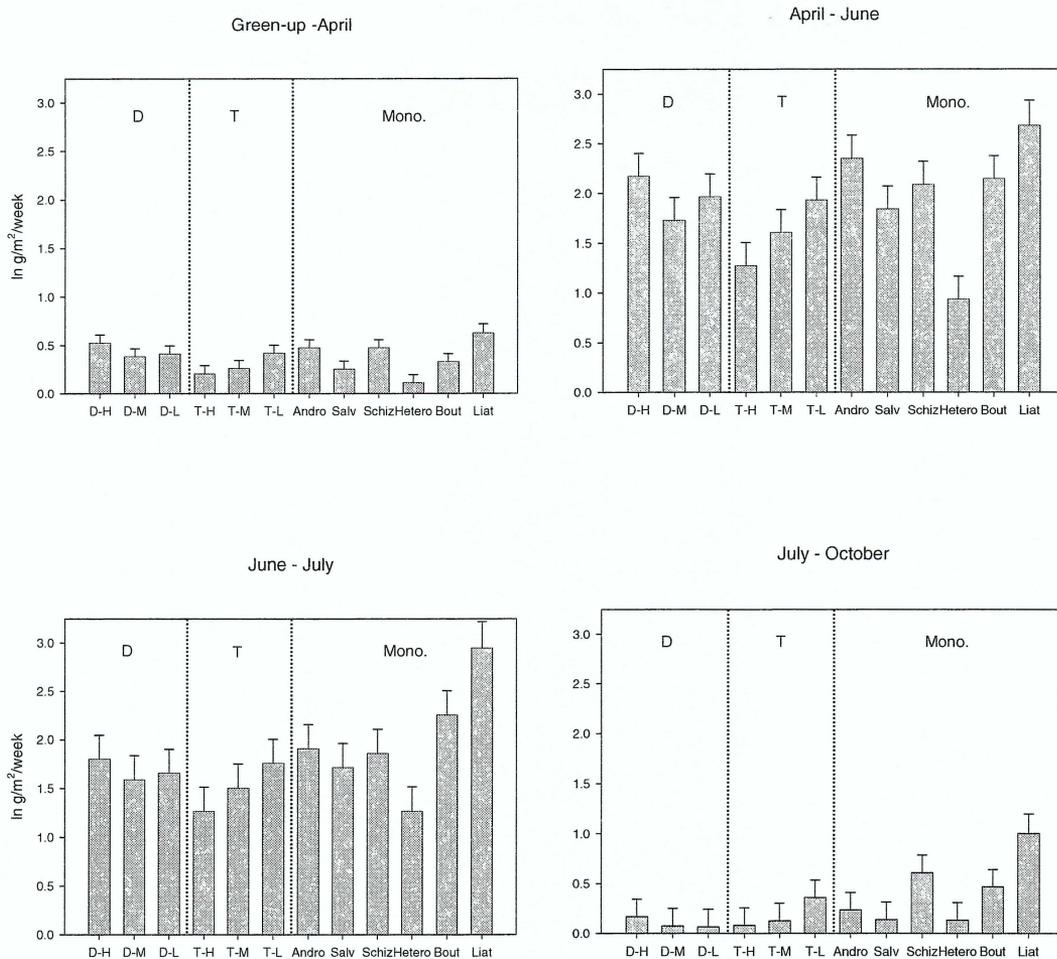


Figure 2. Mean (Lsmeans + standard error) rate of invader biomass accumulation across 2004 and 2005 in 4 species mixtures planted at three levels of evenness (H, M, L) and with all tall species (T) or species with dissimilar heights (D), or planted in monoculture, in a field experiment in Western Iowa. Abbreviations for the monocultures are: Andro- *Andropogon gerardii*, Salv- *Salvia azurea*, Schiz- *Schizachyrium scoparius*, Hetero- *Heterotheca villosa*, Bout- *Bouteloua gracilis*, and Liat- *Liatris punctata*.

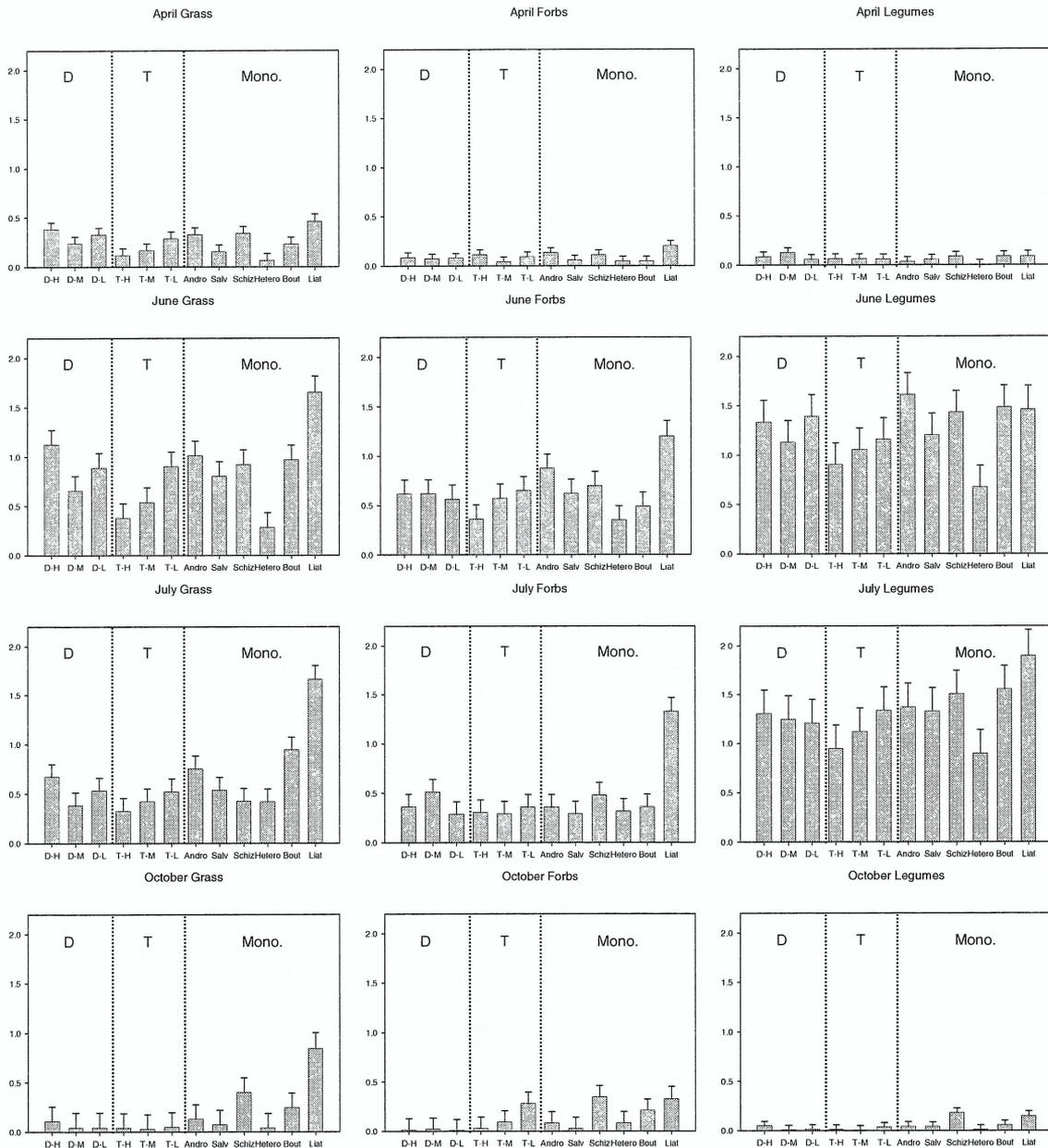


Figure 3. Mean rate of invasion by taxon at each weeding date across 2004 and 2005 in a planted field experiment in western Iowa. The y-axes are $\log \text{g/m}^2/\text{week}$ invader biomass.

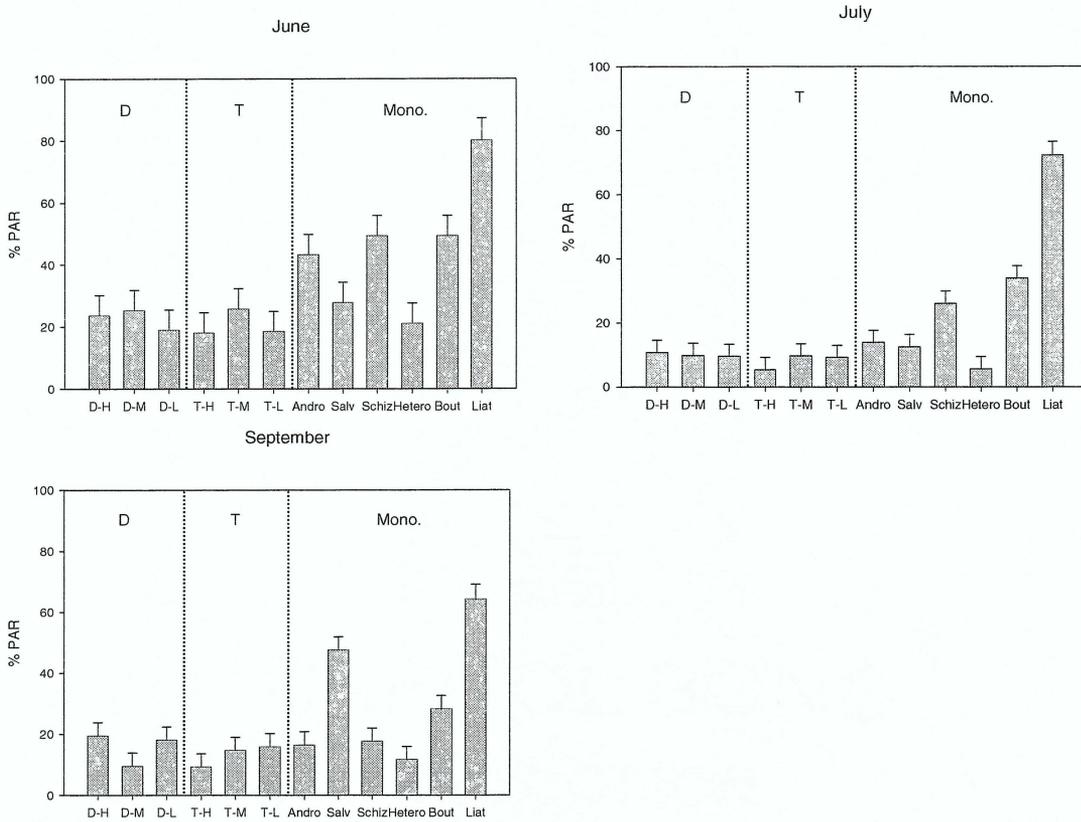


Figure 4. Mean rate of light penetration, as percentage of total photosynthetically active radiation, across 2004 and 2005 in each plot type at each sampling time in a planted field experiment in Western Iowa. Abbreviations are as in Figure 2.

CHAPTER 3. MODES OF INVASION AND PERSISTENCE OF AN EXOTIC, CLONAL LEGUME SPECIES

A paper to be submitted to an international journal

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Abstract

Plant invasions have been hypothesized to proceed at the local, i.e. individual patch or stand, scale according to one of several distinct spatial patterns. However, few studies have attempted to reconstruct the patterns of perennial herbaceous plant invasions at local scales due to difficulty in determining the age of individuals. We used herb chronology to determine the ages of roots within several crown vetch (*Coronilla varia* L.) patches in order to characterize the spatial age structure of these patches. Additionally, we examined both sexual and vegetative crown vetch reproduction, with regard to potential impacts on local spread and persistence, through seed bank sampling and greenhouse experiments. We found little distinct spatial age structuring in crown vetch patches, perhaps due to a lack of older roots caused by rapid ramet turnover within patches. We also found no support for the hypothesis, proposed by several land managers, that crown vetch builds up a large seed bank. However, we did find that even small fragments of crown vetch plants are capable of vegetative regeneration, which may be important in explaining this species' persistence in spite of control measures.

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Introduction

As the spread of exotic organisms has generated increasing environmental concern (Vitousek et al. 1996), researchers have worked to document the patterns of past and present invasions (Pysek et al. 1998) and to generate models capable of predicting future ones (Hastings 1996). These patterns, and likely the processes causing them, have proven to be highly scale dependent (Collingham et al. 2000, Levin 1992).

It has been possible to reconstruct patterns of invasion at large geographic scales from herbarium records and other sources (Weber 1998). The rate at which many invaders spread can often be accurately modeled at regional scales using simple reaction-diffusion models that assume dispersal and movement are random (Skellam 1951, Andow et al. 1990, van den Bosch et al. 1992). However, when applied at more localized scales these models have yielded mixed results. Frappier et al. (2003) found that a diffusion model accurately described the spread of a stand of buckthorn (*Rhamnus frangula* L.) in New Hampshire, but Lonsdale (1993) found that simple diffusion models were inadequate when examining the spread of *Mimosa pigra* L. from a wetland in Australia. Both of these studies focused on invading woody plants in situations where the progress of the invasion could be reconstructed by aging stem cross sections or observing aerial photographs. Few studies have attempted to reconstruct the patterns of perennial herbaceous plant invasions at local, i.e., individual patch or stand, scales due to difficulty in determining the age of individuals (Dietz 2002).

If the spatial spread of invasives across a landscape can be predicted accurately by models that assume movement is random, then the models are useful without further complication (Andow et al. 1990). However, movement is clearly not random. Plant dispersal

and recruitment are greatly effected by micro site variation (Kadmon and Shimda 1990) and neighbor effects (Barton 1993). Understanding the movement of invaders at a finer scale may help us understand the processes that govern invasions. Clonal plants may be particularly useful study organisms in examining localized patterns of invasion, as they have the ability to respond to local conditions by selectively placing ramets in favorable sites (Evans and Cain 1995, Van Klunen and Fischer 2001).

Lovett Doust (1981) proposed two possible contrasting invasion patterns for clonal species. She described species that would advance as tightly packed fronts, a “phalanx pattern,” as one extreme, and species that would spread out into the surrounding vegetation to minimize intraspecific contact, a “guerilla pattern,” as another. Wilson and Lee (1989) expanded the concept of guerilla and phalanx invasion patterns beyond clonal species to include all plant invasions and added the term “infiltration invasion” to describe a pattern where both short distance dispersal (typical of a phalanx pattern) and long distance dispersal (typical of a more guerilla like pattern) occur simultaneously. These patterns could potentially occur at either the scale of individual populations or at much larger landscape scales. Identifying by which, if any, of these patterns an individual population has expanded could provide valuable insight into the processes that prevent or allow a species to spread locally (Dietz 2002). Additionally, if the pattern by which a population is expanding is close to the phalanx or infiltration pattern, it should be possible to estimate the rate of spread of the population from the spatial-age structure (Dietz 2002).

This paper details a series of observational studies and controlled experiments aimed at furthering understanding of the dynamics of crown vetch (*Coronilla varia* L.) invasions. In one study we used herb chronology, a recently developed technique for aging herbaceous

perennials (Dietz and Ullmann 1997), to age individual crown vetch plants. We tried several sampling patterns in different patches of crown vetch in order to describe the patterns by which the patches had spread. We also made detailed maps of the borders of individual patches within a site, and remade the maps one year later to observe changes in patch boundaries through time. Additionally, we examined both sexual and vegetative crown vetch reproduction with regard to potential impacts on local spread and persistence, through seed bank sampling and greenhouse experiments.

Study System

THE PLANT

Crown vetch (*Coronilla varia* L.) is a herbaceous perennial legume native to the Mediterranean region. Its trailing stems form dense patches in which very few other species are found. Crown vetch spreads by seed and asexually, and is now widespread in the United States, being found in all lower 48 states except Louisiana, North Dakota and California according to the USDA's plant distribution maps (plants.usda.gov). It has been widely used as a ground cover and for erosion control, and was heavily planted along roadsides between the 1950s and 1980s. However, it has fallen out of favor as its effectiveness in erosion control has come into question (USDA 2002). Crown vetch also competes with more desirable native vegetation (Walck et al. 1999, Symstad 2004) and can spread away from roadsides and into natural areas (Solecki 1997). It is difficult to eradicate once established, and prairie reconstruction near or on roadsides can be made difficult or impossible in areas with large crown vetch populations (Shirley 1994).

STUDY SITES

Field work was conducted at a site (42.08° N, 93.94° W) in Boone County, Iowa, and at Iowa State University's western research farm (42.07° N, 95.84° W) in Monona County, Iowa.

Boone

The Boone site is approximately a half-acre of un-maintained land adjacent to the Des Moines River and the city of Boone's water purification plant. Vegetation at the site is a diverse mix of native and introduced species. While introduced forage grasses such as *Bromus inermis* Leyss. and *Poa pratensis* L. are prevalent, there are also many prairie grasses such as *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, *Schizachyrium scoparium* (Michx.) Nash, and *Panicum virgatum* L. at the site. The forb community includes some native genera including *Silphium* L., *Verbena* L., *Solidago* L. and *Helianthus* L., as well as a wide variety of weeds and introduced species such as *Cirsium arvense* (L.) Scop., *Rosa multiflora* Thunb., *Lotus corniculatus* L., and *Ambrosia* L.. The site also contains extensive patches of crown vetch (Fig.1). It is unlikely that crown vetch was seeded directly into the site, but it was probably seeded along a county road that borders the site. These intentionally planted populations are the most likely original propagule source for the patches now invading this site.

Western Research Farm

Iowa State's western research farm is located in the loess hills region of Iowa. The crown vetch patches used in seed bank sampling are in a pasture located adjacent to a roadside ditch containing crown vetch. Prior to 2002, the pasture was dominated by smooth brome (*Bromus inermis* Leyss.). In 2002 the area was treated with herbicide, plowed under,

and planted with prairie species as part of a restoration study. Many weeds came into the pasture after it was planted, but crown vetch was not one of the early invaders and by the end of 2003 was still present only in trace amounts. However, in 2004 crown vetch became a major problem. By May 2005, dense patches of crown vetch had formed so that it comprised 46% of the vegetative cover in the restoration experiment. Smooth brome had also become quite prevalent, and these invaders forced the abandonment of the experiment (B. Wilsey unpublished data).

Methods

SPATIAL-AGE STRUCTURE

We characterized the spatial-age structure of three crown vetch patches at the Boone site. We hypothesized that roots of similar ages might be clustered together in relatively distinct regions of the patches, and that locating and delineating these regions would provide insight into the pattern of spread that had led to the current patch dimensions. As we had no reasonable way of forming *a priori* hypotheses about the relative sizes or locations of these regions within patches, we tried different sampling methods in each patch in order to get an idea of what type of sampling design would be most appropriate for future work.

The smallest patch sampled (patch 1) measured roughly 3 x 3.5 m. Seventy-three 0.25 m² quadrats were sampled within this patch. Quadrats were placed directly adjacent to one another, for complete coverage of about 2/3 of the total patch. All roots were dug up within each quadrat. The age of each root was determined by counting annual growth rings in cross sections of the root, using the methodology of Dietz and Ullman (1997).

The second crown vetch patch (patch 2) sampled was roughly twice as large as the first. A 6 m transect was run across the center of the patch. Five transects were run across the patch perpendicular to the 6 m main transect, crossing it at 1 m intervals. All transects were sampled every 0.5 m. The sampling procedure consisted of removing one shovel full of soil and extracting all crown vetch roots from it. The largest of these roots were then aged.

The third patch (patch 3) sampled was quite large. A 22 m long transect was run across the center of the patch, and a second 20 m long transect was run perpendicular to this transect so that it crossed at the midpoint in the center of the patch. The sampling procedure was the same as for the second patch, except that the sampling interval was 1 m instead of 0.5 m.

PATCH BOUNDARY MAPPING

We used a Trimble GeoXT GPS unit with sub-meter accuracy to map the boundaries of all crown vetch patches at the Boone site on August 31, 2004, and again on August 29, 2005. On each of these days we walked through the site attempting to find all crown vetch patches. At each patch, we slowly walked around the patch outline while recording our path with the GPS unit. These data were recorded as shape files and then imported into ArcView 9.0. In ArcView, we calculated the area of each shape file. These areas were summed in order to obtain the total area covered by crown vetch patches in each year. Our goal was to examine year-to-year variation in total patch size in order to see if crown vetch was actively taking over more of the site.

SEXUAL REPRODUCTION

Seed Depth and Emergence

In order to examine the ability of crown vetch seedlings to emerge from different soil depths, we conducted a greenhouse study using commercially purchased crown vetch seed from Nature's Own (Manteno, Ill.). We seeded 30 pots with 25 crown vetch seeds per pot. These 30 pots were divided into three treatment groups of 10 pots. In the first treatment, the seeds were placed with tweezers approximately 1-2 cm below the potting soil surface. In the second treatment the pots were filled with soil to a point 4 cm below the lip of the pot, the seeds were added, and then the pots were filled with packed potting soil up to the lip. In the third treatment the seeds were 8 cm below the lip of the pot. Pots were placed in random order on a greenhouse table, kept watered, and monitored for seedling emergence for 8 weeks. Seedlings were removed as they emerged to avoid any reduction in emergence due to intraspecific competition. Seedling emergence was compared between treatments with SAS ANOVA and Tukey-adjusted comparisons of means.

Seed Bank

Two studies were conducted to examine the distribution of crown vetch seeds in the soil seed bank at the Boone site and at the Western Research Farm.

At the Boone site, on May 19, 2005, one 41 m long transect was placed through a large patch of crown vetch and out into an area with smaller scattered crown vetch patches. We sampled at 22 points along this transect. All sampled points were at least 0.5 m apart, and points were selected so that samples were taken within and on the borders of the large and smaller patches of crown vetch, as well as in areas with other vegetation. At each sampling point two 2.5 cm diameter soil cores were taken to a depth of 15 cm, for a total of 44 soil cores. These cores were separated into 4 layers, the surface layer from 0-2 cm deep, and subsequent layers from 2-6, 6-10 and 10-15 cm deep. These were then bagged and

taken directly to an Iowa State greenhouse. Each of the 176 samples (44 cores x 4 layers/core) was spread out in a 4 inch pot on top of sterilized potting soil. All pots were kept watered and seed germination was recorded weekly. All seedlings were removed when they could be identified to the generic level. Seedlings that became large enough to inhibit the germination of other seeds in the same pot, but that could not yet be identified, were transplanted into separate pots and allowed to continue growing. These seedlings were kept until they could be positively identified, or at least until we could be certain that they were not crown vetch. We ran the experiment for 17 weeks.

The procedure followed at the Western Research Farm pasture was quite similar to the one used at the Boone site, except for the layout of the transects. On June 21, 2005, a 4 m transect was run through a patch of crown vetch. At the 1 and 3 m points along this transect, 3 m long side transects were placed at right angles to the main transect across the patch and out into the adjacent grassland. Each transect was sampled at 0.5 m intervals, with two soil cores being removed at each sampling point. Soil cores were taken to a depth of 10 cm, and divided into three layers 0-2, 2-6 and 6-10 cm deep. A total of 42 soil cores were taken. Each layer from each core was placed in its own pot for a total of 126 pots, and the same procedure described above was followed to determine the number and composition of the viable propagule supply in the soil.

VEGETATIVE REPRODUCTION

Because we found no evidence to support the hypothesis that crown vetch builds up a large seed bank (see results), and because mowing has been shown to be ineffective in crown vetch control (Symstad 2002), we examined the ability of crown vetch to regenerate from vegetative fragments. We clipped plants at ground level and brought them to the lab. Plant

sections in the following categories were cut from the plants: leaflet only, 5-10 cm section of leaf, 2-10 cm long section of stem without a node, and 2-10 cm long section of stem with a node. These sections were then placed in pots on the surface of packed potting soil. Three sections, all of the same type, were placed in each pot. Ten pots were given each section type, for a total of 40 pots. These pots were divided into two sets of twenty pots (5 pots per section type). One set was watered 2 to 3 times per week until the soil was well saturated, the other set was only watered once per week. All pots were on the same table in the greenhouse, but the low and high water treatments were slightly separated in order to avoid incidental watering of the low water treatment. All pots were monitored for one month.

Results

SPATIAL-AGE STRUCTURE

We aged a total of 287 roots from the three crown vetch patches. The majority of these (66%) were only 2 or 3 years old. The root ages from each patch, and the spatial distribution of the oldest roots are shown in figures 2, 3 and 4. There was a weak tendency for roots of similar age to occur close to one another (Figure 5). However, all significant spatial structuring quickly disappears at larger distances (Figure 5). This makes it impossible to discern any clear pattern by which these crown vetch patches may have spread.

PATCH BOUNDARY MAPPING

The total area of all crown vetch patches at the Boone site was 3060 m² in 2004. One year later, this area had increased to 3630 m² (Figure 1). This increase was due to the appearance of several new, small patches as well as the expansion of existing patches.

However, not all of the patches expanded between 2004 and 2005. Some of them contracted, and others shifted location slightly by shrinking on one side while expanding on another.

SEXUAL REPRODUCTION

Seed Depth and Emergence

There were significant differences in seedling emergence among the planting depth treatments ($F_{2,27} = 8.32$ $p = 0.002$). Seedling emergence from a planting depth of 4 cm was significantly higher than from both the surface layer and 8 cm (Tukey adjusted comparisons $\alpha < 0.05$) (Figure 6). Seedling emergence in all treatments was rapid, with 88% of seedlings emerging within the first 14 days after planting.

Seed Bank

The viable seed bank at the Boone site contained an estimated 13,150 seeds/m², while the western research farm site seed bank had an estimated 9,200 seeds/m². Both of these viable seed densities are within the range reported for Great Plains grasslands by Lippert and Hopkins (1950). No crown vetch seedlings emerged from any of the soil samples at either site. Other data on the composition of the seed bank at each site is reported in the appendix.

VEGETATIVE REPRODUCTION

In the high water treatment, all 15 of the stem sections that contained a node survived and produced new growth by sending up shoots from the node. Some of this new growth was visible as early as three days after the experiment began. None of the stem sections without nodes or the leaf sections produced any new growth, but they were still green at the end of the month.

In the low water treatment, several of the stem sections that contained nodes produced new growth, but none of them survived past three weeks. All of the plant sections in the low water treatment were clearly dead by the end of the month.

Discussion

Crown vetch is quite difficult to eradicate once established. One explanation frequently given for the resilience of crown vetch is that it is thought to build up a large and persistent seed bank (The Nature Conservancy 2003). This belief is likely based on the fact that the plants flower and produce seed for nearly the entire growing season. It is usually possible to find both newly opened flowers and mature fruits within a few feet of each other within a crown vetch patch. However, in a study examining interactions between patches of crown vetch and tall fescue along a roadside embankment, Luken (1987) noted that successful recruitment from seed was rare in established crown vetch patches. To our knowledge, our seed-bank sampling represents the first attempt to actually collect data on crown vetch in the seed bank. We were unable to find any viable crown vetch seed in soil samples taken in and around two established crown vetch patches. This result may surprise some land managers, but it is perhaps not unusual given the low rates of sexual reproduction by many clonal species (Harper 1977, Eriksson 1989). We did find extensive systems of underground rhizomes in the patches we sampled, indicating a great deal of vegetative reproduction was taking place. Through our greenhouse study, we also documented crown vetch's ability to propagate from fragments of the above-ground stems. Although it is not clear to what extent this actually takes place in the field, it could be the mechanism behind

other experimental results showing that mowing is ineffective as a crown vetch control method (Symstad 2002).

While many crown vetch invasions are probably initiated by seed, as it has been reported to invade sites not directly adjacent to plantings (The Nature Conservancy 2003), asexual reproduction appears to be much more important than sexual reproduction in explaining the persistence and resilience of established patches. Any stem section that contains a node is capable of generating a new plant, provided adequate moisture is present. Keeping crown vetch patches mowed may help prevent the production of seed that could disperse to start new invasions but is unlikely to help eradicate existing patches. Additionally, because very small stem fragments are capable of regeneration, it is highly unlikely that any contact herbicide could kill enough of the stems to prevent a patch from coming back, and even herbicides that translocate throughout the plant may not reach all the plants in a given patch. Repeated control measures in combination with close monitoring will be needed to remove crown vetch from areas where it is undesirable.

There are several patterns by which clonal species have been hypothesized to invade (Lovett Doust 1981). If crown vetch patches spread in distinct patterns, understanding these patterns would be very useful in developing methods for controlling this species. However, we found no such patterns in the spatial age structure of crown vetch patches. We found some weak spatial autocorrelation at very short distances, meaning that roots of similar age were more likely than would be expected by chance to be found close to one another, but this autocorrelation disappeared very quickly as distance increased. Dietz (2002) found strong spatial-age structure in a patch of spotted knapweed (*Centaurea maculosa* Lam.) when he first sampled in 1999. However, when the patch was re-sampled in 2003 it had not expanded

beyond the 1999 boundaries and this structure had disappeared (Dietz 2004). The crown vetch patch boundary mapping we did in 2004 and repeated in 2005 showed that the total area of all crown vetch patches at the Boone site had increased. There did not appear to be a consistent pattern of increase, a few new patches had appeared, and some old patches had expanded while a few had shrunk slightly or shifted. Some of this increase may have been due to sampling error, as it is possible that we did not find every small patch present at the site in 2004. However, it seems unlikely that sampling error could explain all of the increase, especially since some of the larger patches have clearly expanded quite a bit. If the older crown vetch patches have reached some sort of dynamic equilibrium with their surroundings and only expand and contract in response to annual variation in local conditions, then natural population turnover as older individuals within the patch die and are replaced could destroy any spatial-age structure that may have been present as the patches were initially expanding. This would imply that models of invasive spread based on simple patterns or random movement and the rate of population increase may give accurate predictions initially (Andow et al. 1990), but that these predictions may become less and less accurate as the invasion progresses and interactions between new invaders, established members of the invasive population and the surrounding habitat increase. However, the lack of distinct spatial patterns in root ages in these crown vetch patches may simply result from the fact that the majority of roots sampled (66%) were only 2-3 years old. Ramet turnover within crown vetch populations may simply be too fast for much spatial-age structuring to develop.

Acknowledgements

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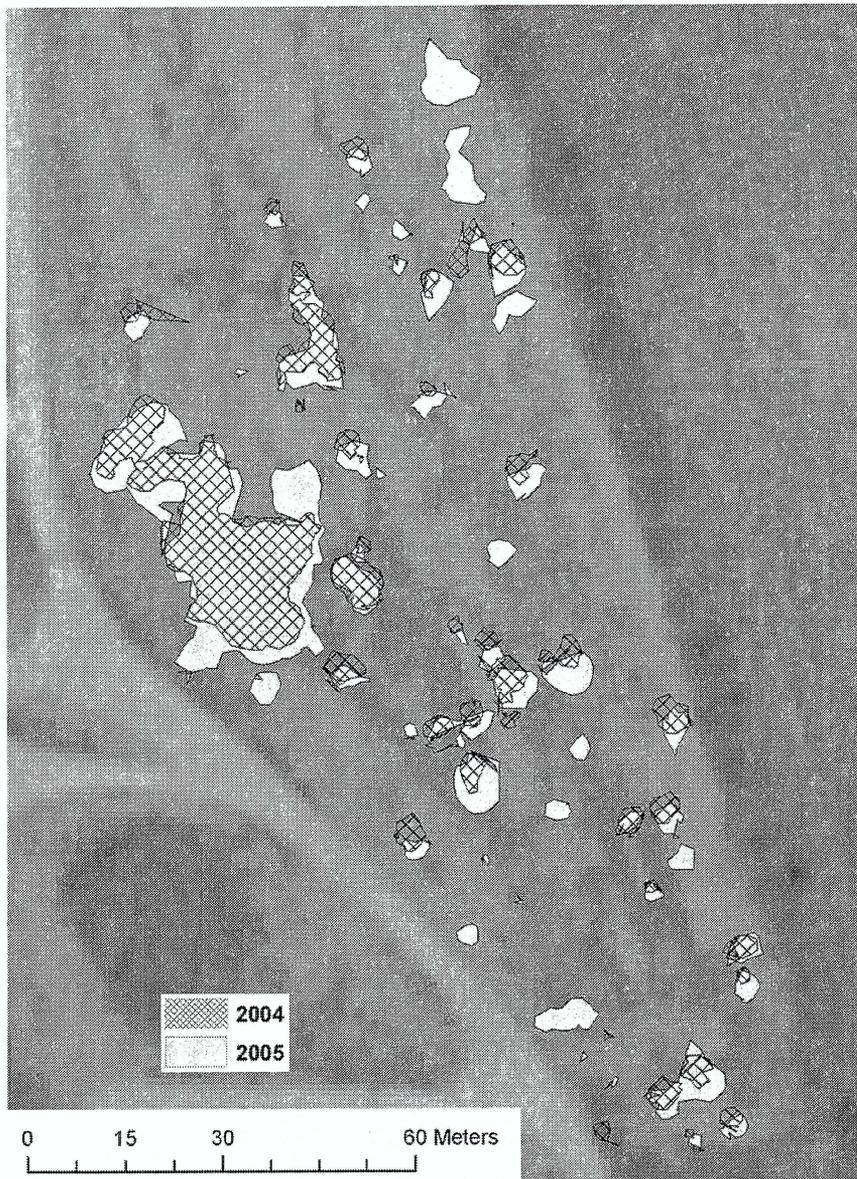


Figure 1. Crown vetch patches at a site in Boone County, Iowa. Patch outlines were mapped in August 2004 and again in August 2005.

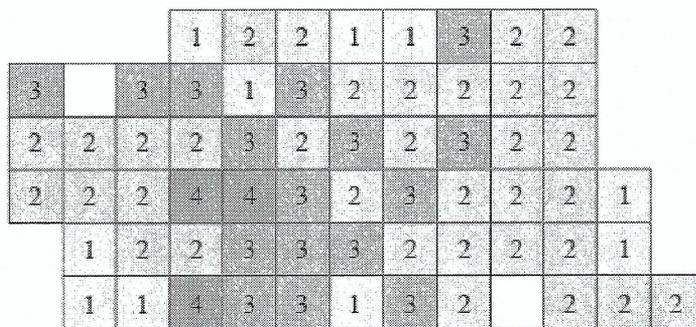
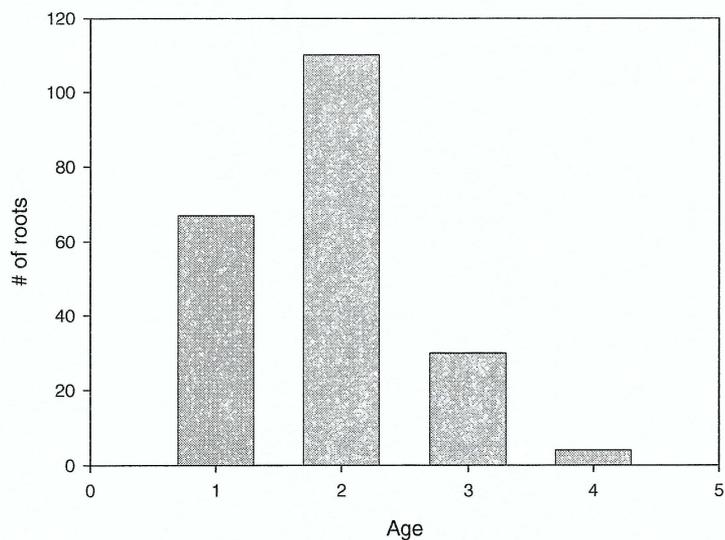


Figure 2. Ages of all crown vetch roots sampled in a patch (patch 1) in Boone county, Iowa. The bar graph shows the ages of all roots. Each box represents one 0.25m² quadrat. The number shown in each quadrat is the age of the oldest root found within that quadrat. The two empty boxes are quadrats that contained no crown vetch.

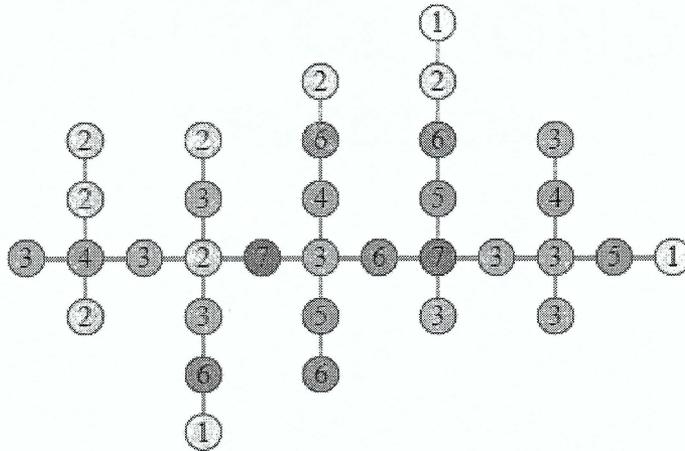
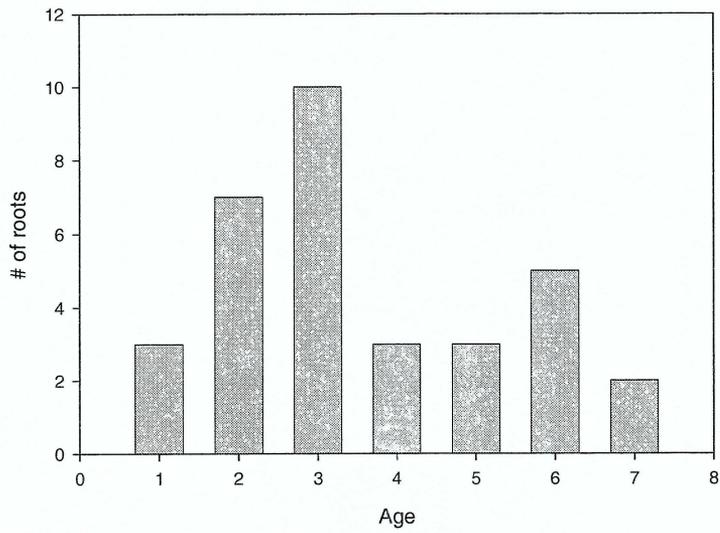


Figure 3. Ages of the oldest roots at each sampling point, and the spatial-distribution of the ages, in a crown vetch patch (patch 2) in Boone County, Iowa. Each line segment represents 0.5 m.

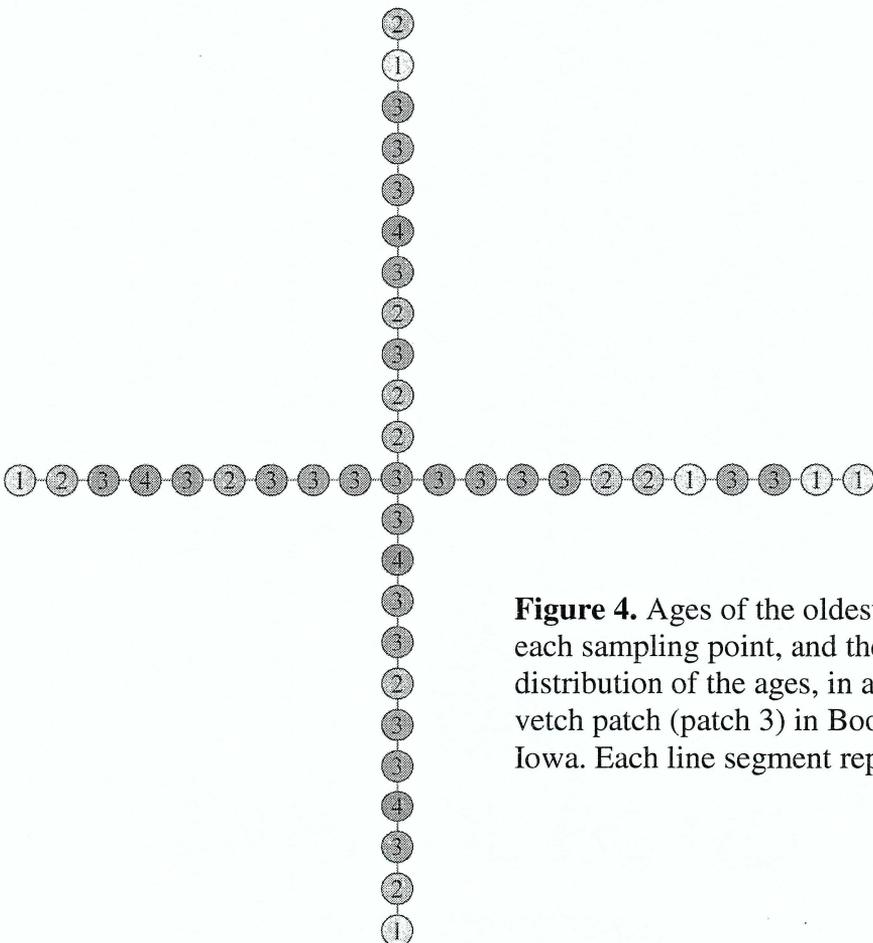
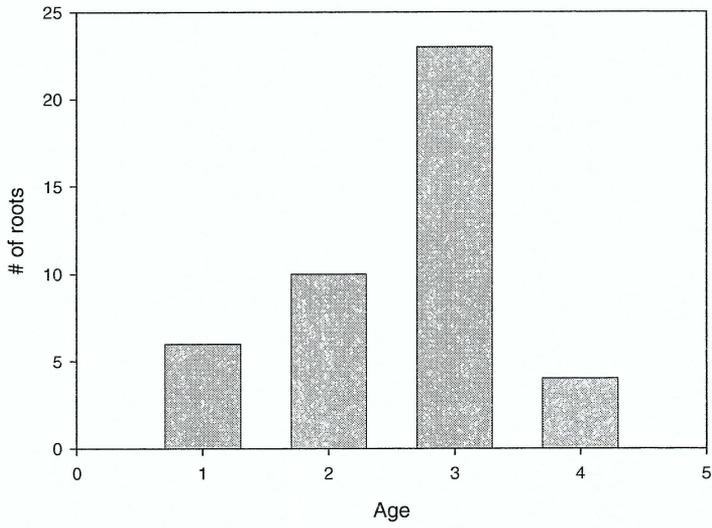


Figure 4. Ages of the oldest roots at each sampling point, and the spatial-distribution of the ages, in a crown vetch patch (patch 3) in Boone County, Iowa. Each line segment represents 1 m.

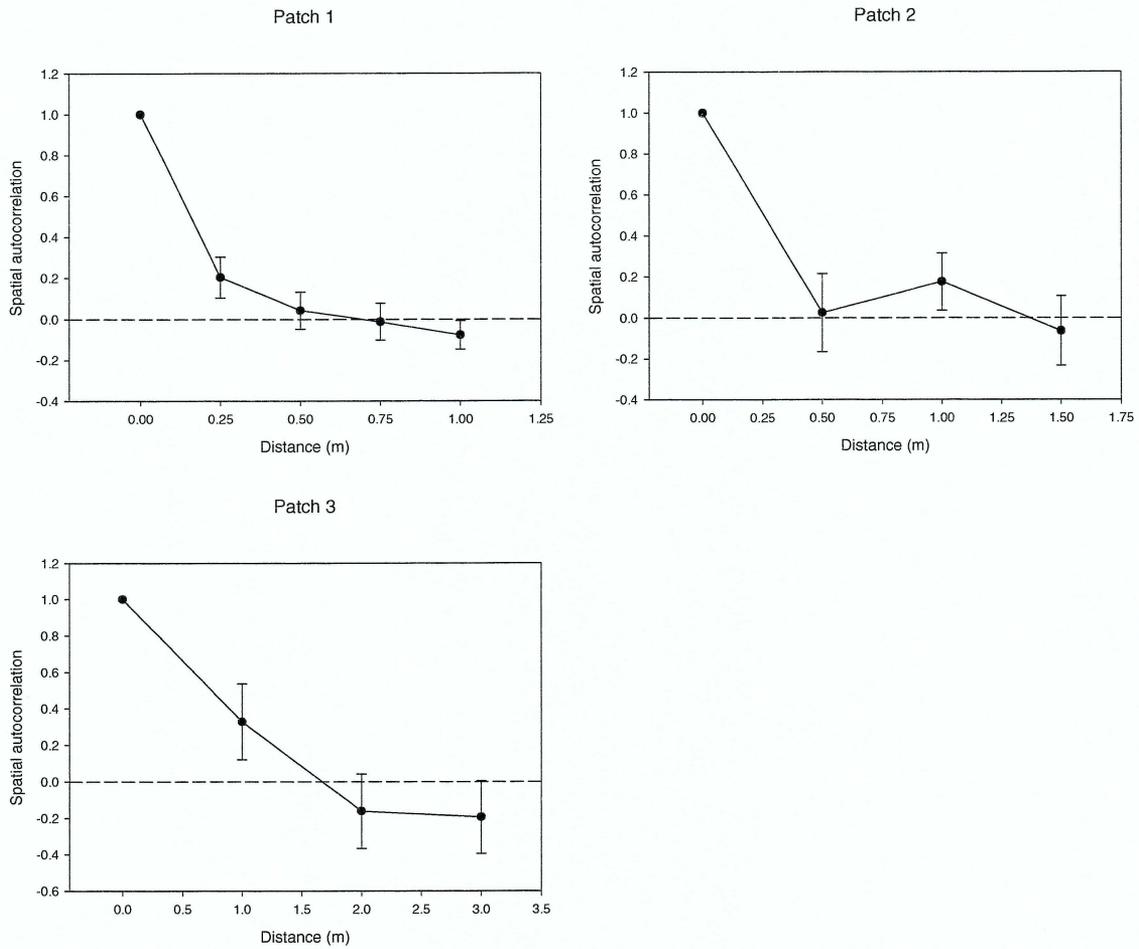


Figure 5. Spatial autocorrelation between root age and the age of surrounding roots in 3 patches of crown vetch at a site in Boone County, Iowa. Error bars represent 95% confidence intervals and the dotted line is at zero..

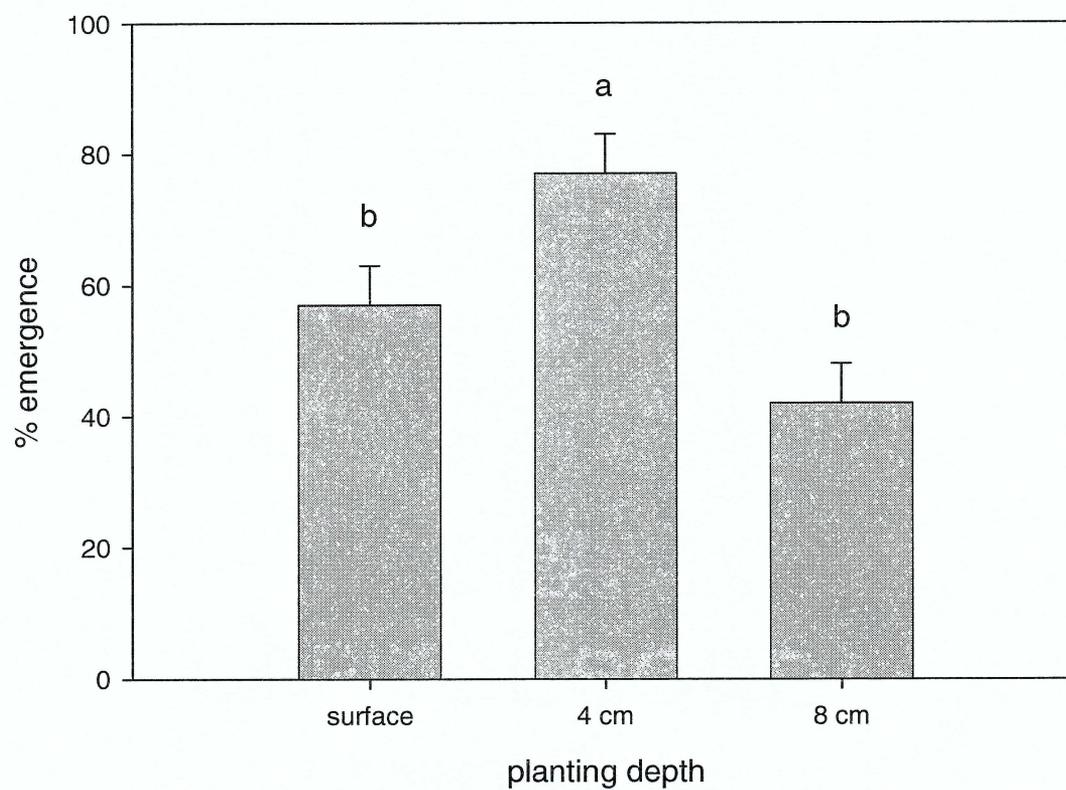


Figure 6. Crown vetch seed depth and seedling emergence in a greenhouse study. Bars with the same lower case letter above are not significantly different at $P = 0.05$.

CHAPTER 4. GENERAL CONCLUSIONS

The relationship between biodiversity and ecosystem functioning has become an important area of research as we have begun to realize the extent to which human actions are changing biodiversity, both through increased extinctions and the widespread introduction of species outside of their native ranges (Chapin et al. 2000). The first part of my research focused on the relationship between diversity and the invasibility of grassland communities, and the second examined modes of invasion of one particular species, crown vetch (*Coronilla varia* L.) in these communities.

The main finding in the first part of my research was that the relationship between diversity and invasibility in a given community varies depending on the attributes of the members of that community. Lowering diversity by removing short species from big bluestem (*Andropogon gerardii* Vitman) dominated communities had no effect on the invasibility of these communities. However, removing tall species from these communities did cause an increase in invasibility. This was contrary to expectations, as removing short species lowered the amount of height dissimilarity present in the communities, which would be expected to reduce niche complementarity and increase invasibility (Stachowicz and Tilman 2005).

While we found no support for niche complementarity through height dissimilarity, we found some support for niche complementarity through phenology. The vast majority of the invaders in our experimental prairie communities appeared in the spring and early summer. Communities that contained species that were actively growing and competitive at this time were better able to resist invasion. The practical implication of this result for prairie managers is that management regimes favoring warm season grasses may lead to reduced

resistance to invasion by cool season forbs and grasses, which make up a substantial portion of the weed flora in many prairie areas.

In the second part of my research, I had originally intended to compare crown vetch invasion patterns in areas dominated by introduced species to patterns in prairie restorations in order better understand community effects on invasion by this exotic legume species. This turned out to be impossible. I had intended to work along roadsides, where there have been many attempts at prairie restoration recently. Unfortunately, this did not work out as there were few suitable sites available. Many of the attempted restorations had simply failed, and were now dominated by exotic species—usually smooth brome grass (*Bromus inermis* Leyss.). Additionally, when I did try to reconstruct patterns of crown vetch invasion by aging roots within crown vetch patches, I found little distinct spatial age structuring. This may have been to a lack of older roots caused by rapid ramet turnover within patches.

As I began to further investigate crown vetch invasions, I found several problems with the little information that was available about this plant. For example, it is widely reported that crown vetch was first introduced to the United States in the 1950s. However, the Ada Hayden Herbarium at Iowa State University has a specimen of crown vetch collected in Connecticut in 1899 and several specimens collected in Iowa in the 1920s and '30s.

Crown vetch has proven difficult to eradicate once established. A commonly believed explanation for this is that it builds up a large and persistent seed bank (The Nature Conservancy 2003), but I was unable to find any published studies in which anyone had actually sampled the seed bank in areas invaded by crown vetch. When we did sample the seed banks at two sites with large crown vetch populations, we found absolutely no crown vetch seedling emergence. However, we did find that even small fragments of crown vetch

plants are capable of vegetative regeneration, which may be important in explaining this species' persistence in spite of control measures.

Future Considerations

The idea of niche complementarity through functional dissimilarity is widely prevalent in the ecological literature. However, models based on this idea are usually incapable of generating accurate predictions for specific communities (Stohlgren et al. 2003, Brown and Peet 2003). This is because the term "functional dissimilarity" is too general to be specifically applicable. In order to make accurate predictions, we need more detailed studies of plant communities and the individual species of which they are comprised. This may allow us to eventually state, for a given community, which functional attributes of the species present have what effects on ecosystem processes. While gathering this information would require an extensive amount of fieldwork, it would be an invaluable aid in developing both our understanding of plant communities and our ability to manage them wisely.

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APPENDIX. COMPOSITION OF THE SOIL SEED BANK AT THE BOONE SITE AND WESTERN RESEARCH FARM

Identities, to the generic level or lowest taxonomic rank that could be determined, and relative abundances (percent of total seedlings from the site) of all seedlings emerging from soil cores taken in two study sites with large crown vetch populations.

Boone

Taxa	% of total
Unknown (not crown vetch) Dicots	41
<i>Chenopodium</i>	16
<i>Potentilla</i>	14
Unknown Poaceae	8
<i>Conyza</i>	7
<i>Rorippa</i>	4
<i>Setaria</i>	3
<i>Erigeron</i>	2
<i>Poa</i>	1
<i>Eragrostis</i>	1
Unknown Cyperaceae	1
<i>Amaranthus</i>	<1
<i>Epilobium</i>	<1
<i>Oenothera</i>	<1
<i>Trifolium</i>	<1
<i>Verbascum</i>	<1

Western Research Farm

Taxa	% of total
Chenopodium	83
Amaranthus	9
Unknown Monocots	6
Unknown (not crown vetch) Dicots	2

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