PLANT-ENVIRONMENT FEEDBACKS IN A NATIVE AND INVASIVE SYSTEM

by

Emily C. Farrer

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Doctoral Committee:

Professor Deborah E. Goldberg, Chair
Professor Knute J. Nadelhoffer
Professor Earl E. Werner
Professor Donald R. Zak

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To Nico, whose help, encouragement, and back rubs made this happen.

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ABSTRACT

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Chair: Deborah E. Goldberg

Individual plants interact through a variety of mechanisms creating plant-soil feedbacks, in which a plant affects the environment, and this change feeds back to influence the performance of that plant and other members of the community. Feedbacks can have consequences at the community and ecosystem levels; however, despite the large body of work on component processes, how measured interactions among individuals actually affect large-scale patterns of species composition, diversity, and invasion remains largely untested. In this dissertation, I use a combination of 1) spatio-temporal surveys and modeling and 2) measurements of interactions in field experiments, to test the mechanisms through which plants interact and the importance of these interactions in driving community structure and dynamics in two systems, temperate wetlands invaded by hybrid cattail and native dry grasslands. Positive feedbacks are predicted to be important for explaining dominance of invasive species, because modification of the environment to their own benefit would further their invasion.

Negative feedbacks are predicted to dominate in native systems where they lead to limitation of conspecific growth, promoting coexistence. In the invaded system, experiments suggest that hybrid cattail (*Typha x glauca*) produces positive feedbacks: it increases nitrogen cycling twofold and decreases light through high litter production, an environment in which cattail performs well but native species decline. These positive feedbacks could contribute to the pattern found in field surveys that *T. x glauca* was associated with locally high soil nutrients, low light, and large amounts of litter, and that native diversity was highest in areas of shallow litter depth. In the native grassland system, both transplant experiments and fitting models to survey data suggest that negative feedbacks are common: conspecifics inhibit the individual and population growth of each of the dominant species more than heterospecifics. The intermediaries in these negative feedbacks include soil nitrate and light reduction, however other unmeasured soil properties, such as pathogens or mycorrhizae, also likely play a role. Overall, this suggests that the balance of interactions may shift from negative feedbacks in native systems to positive in invasive systems, which contributes to the coexistence among natives and dominance of invasives.

CHAPTER I

Introduction

Individual plants interact through a variety of different mechanisms, and these interactions can have consequences at the community and ecosystem levels. However, despite the large body of work on components of plant interactions, how measured interactions among individuals actually affect large-scale patterns of species composition, diversity, and invasion remains largely untested. For example, experimental research on competition, facilitation, and plant-soil feedbacks has typically assessed individual growth under controlled conditions over a single or few growing seasons (Goldberg and Barton 1992, Gurevitch et al. 1992, Maestre et al. 2005, Brooker et al. 2008, Cahill et al. 2008, Kulmatiski et al. 2008). It is therefore unclear whether these types of interactions have community consequences in the field, in which many other processes, such as disturbance, herbivory, dispersal limitation, and neutral dynamics, undoubtedly occur. This dissertation develops a framework integrating 1) spatio-temporal field surveys and 2) experimental measurement of interactions and intermediaries in the field to explicitly test the mechanisms through which plants interact and the importance of these interactions in driving community structure and dynamics in two systems, temperate wetlands invaded by hybrid cattail and native dry grasslands.

Historically, the main types of species interactions, studied empirically and theoretically, were resource competition and other trophic interactions. However, individuals interact in many ways other than through resource uptake. Plants can affect the soil through root exudation, soil aeration, and attraction of pathogens or mycorrhizae. Many nontrophic processes for plants occur through litter deposition, which alters the environment through shading, temperature amelioration, moisture retention, and nitrogen mineralization during decomposition. The importance of litter in plant interactions and community structure has received some attention in the ecological literature, however many studies are restricted to recruitment stages (Facelli and Pickett 1991). Overall, nontrophic processes have not been fully integrated into the study of plant interactions and often are studied separate from resource reduction.

These interactions can be integrated in a broader context as plant-environment feedbacks, in which a plant alters the environment in ways that feed back to influence the performance of that plant and other species. The net effect of one plant on another is thus composed of two components, plant effect on the environment and plant response to that altered environment (Fig. 1.1, Goldberg 1990). Plants create feedbacks through the effects of live processes and litter on different intermediaries both abiotic and biotic (Bever 1994, Bever et al. 1997, Ehrenfeld et al. 2005). Feedbacks are positive if they increase plant performance relative to other species, or negative if they decrease relative plant performance (Bever et al. 1997). For example, a species might negatively affect the environment by reducing resources to low levels; however if it is the best competitor under low resource conditions compared to other species in the community, this produces a positive feedback.

Theoretical studies have shown that the types of feedbacks displayed by species in a community have consequences for the structure and dynamics of the system. Both classic competition theory and more recent models of niche partitioning and feedbacks demonstrate that even small magnitudes of negative feedback can promote long-term species coexistence; in other words stable coexistence is possible if intraspecific competition is greater than interspecific competition (Tilman 1982, Bever et al. 1997, Chesson 2000, Bonanomi et al. 2005). Conversely, most models of positive frequency dependence lead to monodominance of a single species, although spatial models indicate that competitive exclusion is slowed if species have similar magnitudes of positive feedback (Molofsky et al. 1999, Molofsky et al. 2001, Molofsky and Bever 2002).

Empirical data are partially consistent with predictions from theory. Plant-soil feedback experiments suggest that negative feedbacks are common in native systems (Kulmatiski et al. 2008); however most competition studies do not find evidence for intraspecific competition being greater than interspecific competition (Goldberg and Barton 1992, Gurevitch et al. 1992, Cahill et al. 2008). Experiments also suggest that invasive species tend to promote positive feedbacks (Klironomos 2002, Sperry et al. 2006, Vinton and Goergen 2006, Van der Putten et al. 2007, Van Grunsven et al. 2007). However, these experiments are often not integrated with field studies of community structure and dynamics in the same system, which could account for studies in which experimental results do not match theoretical predictions.

In this dissertation, I examine plant interactions and feedbacks in a native grassland and an invaded wetland system. I measure the intermediaries that are potentially important in the interaction, including nutrients and light, and I measure consequences of the feedback for the species creating the feedback, for other members of the community, and for the structure and dynamics of the system as a whole. Since invasive and native systems are predicted to have different types of feedbacks, I hypothesize that positive feedbacks will dominate in an invasive cattail system, while negative feedbacks should occur in a native grassland system. This dissertation is divided into three primary chapters. Chapter II explores plant-environment feedbacks produced by invasive cattail, *Typha x glauca*, examined in a survey of invasion and in a transplant experiment. Chapters III and IV examine feedbacks generated by the largely native dominants of a dry sand prairie. Chapter III describes a detailed spatio-temporal survey and model fitting techniques used to estimate interactions, competitive or facilitative, among the four dominant species. Chapter IV tests the direction of interactions among three of the species in a field experiment, and determines whether abiotic intermediaries play a role in driving these interactions. The surveys and experiments performed in each of chapters are illustrated in Fig. 1.2.

Chapter II. Litter drives ecosystem and plant community changes in cattail invasion. If invasive species modify the environment to their own benefit, this can further invasion and lead to suppression and decline of native species. Thus positive feedbacks are predicted to be important in invasive systems (Ehrenfeld et al. 2001, Ehrenfeld 2003, Levine et al. 2006). Invaded systems are indeed commonly associated with a change in environment and a decline in native species diversity; however, many different causal pathways linking these three factors could produce this pattern. The initial driver of environmental change may be anthropogenic or it may be the invader itself, and the mechanism behind native species decline may be the human-induced environmental change, competition from the invader, or invader-induced environmental change (nontrophic effects). I examined applicability of each of these alternate pathways in Great Lakes coastal marshes invaded by hybrid cattail (*Typha x glauca*).

I performed a field survey of three marshes, examining patterns among *T. x glauca* and native species abundance and diversity as well as their associations with environmental characteristics such as soil nutrients, temperature, and amount of litter (Fig. 1.2a). I then tested whether live *T. x glauca* plants or their litter induced changes in the environment and diversity with a live cattail / cattail litter transplant experiment (Fig. 1.2b). If the experimental manipulations of cattail or its litter produce the same effects as the large-scale patterns found in the survey, this is a strong argument for cattails as the mechanism of environmental change and species decline.

Chapter III. Time lags and the balance of positive and negative interactions in driving grassland community dynamics. In order to test whether individual plant interactions and feedbacks have community consequences, it is necessary to quantify the patterns in population dynamics that occur in the field. One way to assess population level interactions is to fit dynamical models to spatio-temporal survey data. Recent studies have used this approach and have found that negative interactions predominate (Law et al. 1997, Freckleton and Watkinson 2001, Adler et al. 2006), despite much evidence that facilitative interactions occur simultaneously with competition (Bertness and Callaway 1994). This suggests that more complex models may be necessary to uncover facilitative effects. In this chapter, I fit models including seasonality, interannual variation, and time lags to survey data to test for patterns in positive and negative interactions among coexisting dominants in a dry sand prairie in Michigan (Fig. 1.2c). The relative strength of conspecific and heterospecific interactions in the community will determine the feedbacks, positive or negative, produced by each species. Time lagged interactions are suggestive of litter effects, because litter production is correlated with past population densities.

Chapter IV. A test of competition and facilitation in a dry perennial grassland. Negative feedbacks are a fundamental requirement for most models of local stable coexistence, that is, intraspecific interactions are more negative than interspecific interactions. Both classic pairwise competition experiments and plant-soil feedback experiments have addressed this question, but these two types of experiments have found contradictory results: competition experiments find competitive hierarchies, whereas plant-soil feedback experiments find evidence for negative feedbacks. In this chapter, I take a first step to merge these two perspectives in an experiment in the Michigan dry sand prairie. I perform a transplant experiment in natural field monocultures with live plants so that transplants experience both competition from the neighbor as well as effects from litter and accumulated soil microbial communities (Fig. 1.2e). I ask whether transplants perform best in monocultures of conspecifics or heterospecifics or no neighbor plots. I also measure abiotic environmental characteristics associated with each of these monoculture types (Fig. 1.2d) to determine if species create different microenvironments and which intermediaries play a role in performance and feedbacks.

The strength and direction of these plant-environment feedbacks measured in the transplant experiment can be compared to the feedbacks estimated from the survey data in Chapter III. If feedbacks patterns are similar in both studies, this strongly suggests that measured feedbacks drive population and community dynamics in nature, and proposes intermediaries important in these interactions.

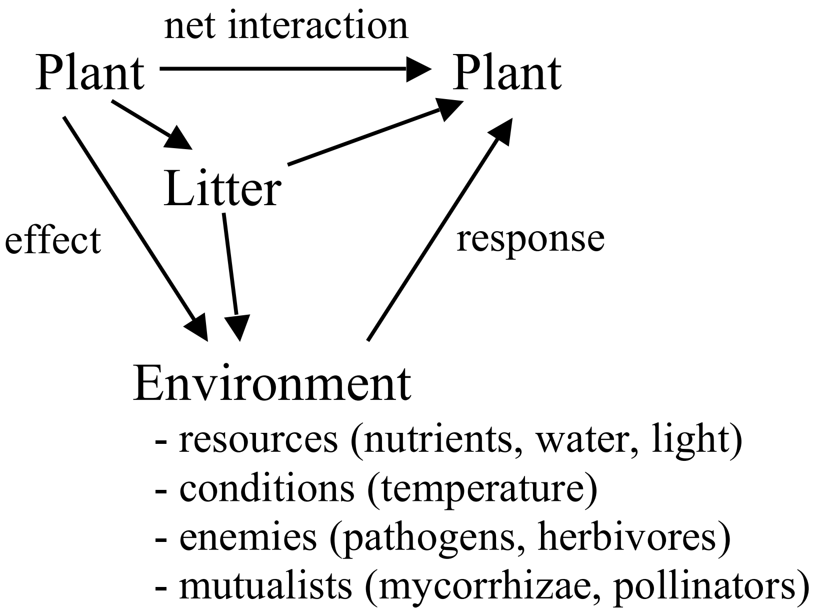

Fig. 1.1. Diagram illustrating plant-environment feedbacks. The net interaction between one plant and another can be described as a feedback, which is composed of two components, plant effect on the environment and plant response to that altered environment. Plants create feedbacks through the effects of live processes and litter on different intermediaries, including resources, conditions, enemies and mutualists.

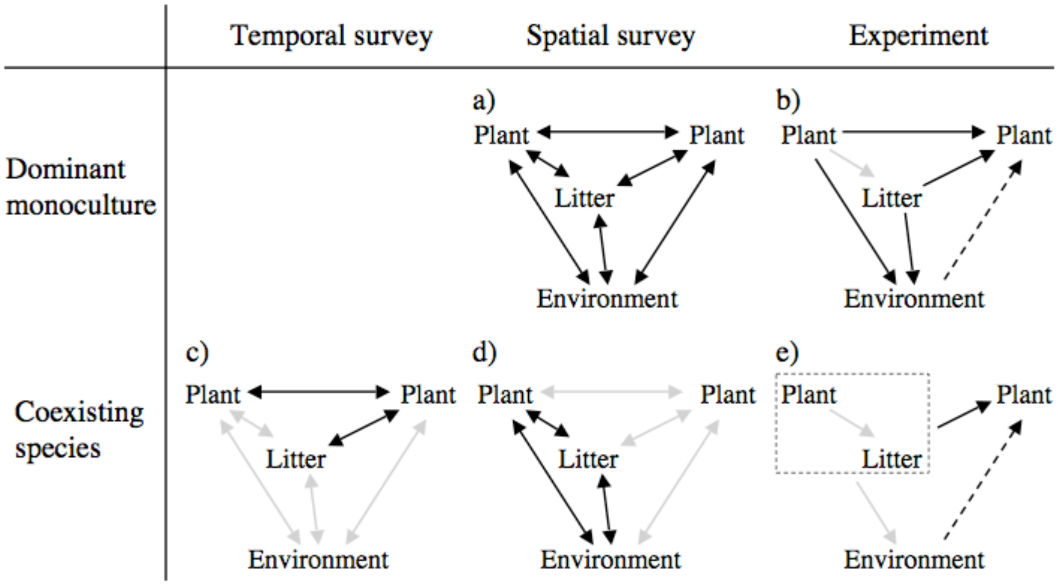

Fig. 1.2. Diagram illustrating the surveys and experiments performed in Chapters 2-4. Black lines indicate interactions that were directly measured; dashed lines indicate effects that were inferred. Double-headed arrows indicate correlations; single-headed arrows indicate that the direction of effect was experimentally determined. For the dominant *T. x glauca* system, Chapter 2 describes a spatial survey which identified correlations among cattails, litter, environmental characteristics, and native plants (a), and a live cattail / cattail litter transplant experiment which tested causal relationships among these factors (b). For the coexisting grassland species, Chapter 3 describes a temporal survey that identified population level relationships among different plant species and litter (c). Chapter 4 describes measurements of environmental characteristics in natural monocultures of grassland dominants (d), and a transplant experiment testing effects of plant/litter field monocultures on other transplanted targets, which was combined with the measurements of environmental characteristics to infer intermediaries (e).

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CHAPTER II

Litter drives ecosystem and plant community changes in cattail invasion

Abstract

Invaded systems are commonly associated with a change in ecosystem processes and a decline in native species diversity; however, many different causal pathways linking invasion, ecosystem change, and native species decline could produce this pattern. The initial driver of environmental change may be anthropogenic or it may be the invader itself, and the mechanism behind native species decline may be the human-induced environmental change, competition from the invader, or invader-induced environmental change (nontrophic effects). We examined applicability of each of these alternate pathways in Great Lakes coastal marshes invaded by hybrid cattail (*Typha x glauca*). In a survey including transects in three marshes, we found that *T. x glauca* was associated with locally high soil nutrients, low light, and large amounts of litter, and that native diversity was highest in areas of shallow litter depth. We tested whether live *T. x glauca* plants or their litter induced changes in the environment and in diversity with a live plant/litter transplant experiment. After one year, *Typha* litter increased soil NH_4^+ and N mineralization twofold, lowered light levels, and decreased the abundance and diversity of native plants, while live *Typha* plants had no effect on the environment or on native plants. This suggests that *T. x glauca*, through its litter production, can cause the changes in ecosystem processes that we commonly attribute to anthropogenic nutrient

loading; and that *T. x glauca* does not displace native species through competition for resources, but rather affects them nontrophically through its litter. Moreover, because *T. x glauca* plants were taller when grown with their own litter, we suggest that this invader may produce positive feedbacks and change the environment in ways that benefit itself and may promote its own invasion.

Introduction

Invaded systems are often associated with a change in ecosystem processes and a decline in native species abundance and/or diversity (D'Antonio and Vitousek 1992, Hobbs and Huenneke 1992, Galatowitsch et al. 1999, Zedler and Kercher 2004, MacDougall and Turkington 2005, Kercher et al. 2007). Managing invaded systems and mitigating negative impacts requires an understanding of the mechanisms driving these relationships. However, because many different causal pathways may link invasion, environmental change, and native decline, it is unlikely that any one set of mechanisms operates in all systems and therefore that management recommendations are similar across systems. Instead, we need to understand the range of causal pathways and, eventually, the conditions under which different mechanisms are more or less important. Figure 2.1 describes a set of conceptual models for the linkages between invasion, ecosystem changes, and native decline based on the combination of the initial driver of the environmental change and the mechanism behind the native species decline.

Environmental change can be initiated by humans or by the invader itself. In *human-directed models* (Fig. 2.1, top row), changes in ecosystem processes are caused anthropogenically, for example by alteration of disturbance regimes (e.g., fire suppression), biogeochemistry (e.g., eutrophication), or hydrology (e.g., wetland draining). This change in environment allows the invader to establish and spread because it may create a temporary resource opportunity (Davis et al. 2000) or because the invader is well adapted to these new conditions (Dukes and Mooney 1999). In *invader-directed models* (Fig. 1, bottom row), the invader establishes at a site due to chance or propagule pressure and, because of physiological differences from the native vegetation, it changes ecosystem processes such as nutrient cycling (Ehrenfeld 2003) or disturbance regime (Mack and D'Antonio 1998).

Independently of the cause of environmental change, native species abundance, diversity, or composition may decline when associated with invasions due to three different reasons. 1) Native species may decline due to the human-induced changes to the environment, if they are not adapted to the human-induced selection regime (Fig. 2.1, column 1) (Byers 2002, Didham et al. 2005, MacDougall and Turkington 2005). This is the same as the “passenger model” of MacDougall and Turkington (2005) in which the invader does not cause native decline at all but is just a passenger in a system already undergoing environmental change. 2) Native species may decline due to competitive pressure from the new invader (Fig. 2.1, column 2). When competition is combined with human-directed environmental change (model 2) this represents the “driver” model of MacDougall and Turkington (2005), in which humans change the environment causing a shift in competitive ability such that the invader is now more competitive than the natives. 3) Lastly, the invader might change the environment in such a way that native species are no longer competitive or able to persist at all (Fig. 2.1, column 3). For example, if the invader's litter reduces light levels or increases sedimentation or anoxia, these nontrophic (non-uptake) effects may inhibit native species.

These five models, differentiated by the combination of the cause of environmental change and the mechanism of native decline, are not mutually exclusive and the relative importance of each pathway may depend on site conditions (e.g., Scott et al. 2001, Ehrenfeld 2003). Despite this complexity, determining the cause and effect relationships among these factors is essential for designing effective management strategies, including conservation and remediation. Knowing the extent to which humans vs. invaders are the cause of environmental change is important for determining if and how human processes should be regulated. Determining the cause of the decline in native species is important for identifying remediation methods. For example, models 2 and 4 suggest only invader removal is necessary to promote the regrowth of native plants; while models 1, 3, and 5 suggest underlying environmental changes must be addressed before the conditions are suitable again for native species (Suding et al. 2004).

In wetland habitats, the most important environmental change associated with invasion and diversity decline is often eutrophication (Galatowitsch et al. 1999, Childers et al. 2003, Zedler and Kercher 2004). Both humans and invaders could potentially initiate this pattern and cause the increase in nutrients. Anthropogenic nutrient input is often assumed to be the cause of elevated nutrient levels and is reasonable in cases where input is known (Davis and Ogden 1994, Drexler and Bedford 2002). However, it is well documented that invasives (Ehrenfeld 2003, Levine et al. 2003), and plant species more generally (Eviner and Chapin 2003), can influence ecosystem processes such as nutrient cycling due to differences in physiology and morphology. For example, invasive wetland plants can stimulate microbial processes via root exudates or through oxygenation of the rhizosphere (Windham and Ehrenfeld 2003). Invasive plants can also increase N cycling through their litter production. Litter with low C:N or low lignin can increase the rate of microbial mineralization because it is easily decomposed and N is quickly made available (Hobbie 1992). Invasives that produce large quantities of litter may also increase N supply in a wetland, because the litter can act as a carbon source for microbes and can retain N in the system in the organic N pool (Bowden 1987).

Eutrophication and invasion in wetlands are often associated with a decline in native species abundance or diversity or a change in species composition (Meyerson et al. 2000, Kercher et al. 2007). However, this relationship is not always quantified (Galatowitsch et al. 1999) and unexpected positive relationships have also been found (Hager and Vinebrooke 2004). Moreover, rarely is the mechanism of species decline investigated (Levine et al. 2003), even though the three causes for the decline in native species in Fig. 2.1 are all plausible. A decline in diversity may result solely from the native community response to elevated nutrients, due to dominance by a particularly productive native species (Green and Galatowitsch 2002). More likely, resource competition from the invader can cause decline of native species. Due to high growth rates and high productivity, invasives such as *Typha* spp., *Phragmites australis*, and *Phalaris arundinacea* are competitive in high nutrient environments and can take advantage of the elevated resources (Galatowitsch et al. 1999, Zedler and Kercher 2004). Numerous fertilization experiments have confirmed this invader growth response coupled with native species decline (Newman et al. 1996, Green and Galatowitsch 2001, Svengsouk and Mitsch 2001, Green and Galatowitsch 2002, Woo and Zedler 2002, Minchinton and Bertness 2003, Rickey and Anderson 2004, Kercher et al. 2007). Thus resource competition from invaders for nutrients or light is a highly probable mechanism for observed declines in native species. Lastly, a decline in natives may also result from nontrophic modification of the environment by the invasive species. Large stands of litter often accumulate when very productive invaders occupy eutrophied environments, and this litter reduces light levels and physically obstructs growth of native species (Hager 2004). These mechanisms of native decline are not mutually exclusive; both resource competition and litter accumulation can concurrently inhibit native species (Lenssen et al. 2000, Minchinton et al. 2006).

The associations among invasion, ecosystem properties, and native plant communities have been well documented. However, the majority of the ecosystem process studies have been non-manipulative surveys; thus they cannot distinguish the direction of causality in invader-environment relationships, nor can they separate the mechanisms behind the associations they see due to the many covarying variables. Likewise, most plant community studies have not separated trophic and nontrophic effects of the invader, and cannot distinguish between strict competitive superiority of the invader or environmental modifications due to litter production.

In this paper, we quantify the field association of invasion, eutrophication, and decline in native species in Great Lakes coastal marshes invaded by *Typha x glauca* Godr. (hybrid cattail). We also test whether *T. x glauca* can be the initial driver of environmental change (does row 2 in Fig. 2.1 occur?) and whether *T. x glauca* affects native species through competition (does column 2 occur?) and/or non-trophic interactions (does column 3 occur?). We assessed the contributions of these models with a transplant experiment using factorial combinations of live *T. x glauca* individuals with or without the addition of *T. x glauca* litter. Invader-directed models (row 2) predict that *T. x glauca* should increase soil nutrients either via its live plants or its litter. If resource competition (column 2) is responsible for native decline, then the live *T. x glauca* treatment is predicted to cause both a decrease in some resource (either nutrients or light) and a decline in natives. If nontrophic effects (column 3) are responsible for native decline, then the litter treatment would be predicted to cause both a decrease in some resource and a decline in natives (i.e., a decrease in abundance or diversity or a change in species composition). Because we tested whether a particular model (or group of models) could occur, and because the models are not mutually exclusive, our approach can support the existence of a contribution from a model but does not reject contribution from other models. Thus this paper is a first, but critical, step in understanding and measuring the many cause-effect relationships in an invasive system, in order to begin to build generalizations about conditions under which different causal pathways are important. Because *T. x glauca* is an important invasive in many wetland systems, these results also have direct management implications.

Methods

Study species – Typha x glauca

Typha x glauca Godr. (hybrid cattail) is an aggressive wetland invasive in North America (Galatowitsch et al. 1999). It is the hybrid between *Typha latifolia* L. and *Typha angustifolia* L. *Typha latifolia*, broadleaf cattail, is native to temperate North America and Eurasia and has a broad distribution on both continents (Grace and Harrison 1986).

Typha angustifolia, narrow-leaved cattail, is not native to the Midwestern United States and was most likely introduced from Europe to the east coast in the early 19th century (Stuckey and Salamon 1987, but see Pederson et al. 2005). It was restricted to salt marshes of the Atlantic coast until the 1880s, was first reported in Michigan in 1900, and now occupies much of the northeast habitat of *T. latifolia* (Stuckey and Salamon 1987, Galatowitsch et al. 1999). These two parent species commonly co-occur in wetlands and readily hybridize; the distribution of *T. x glauca* follows that of *T. angustifolia* as it encounters and hybridizes with *T. latifolia* (Grace and Harrison 1986, Stuckey and Salamon 1987, Galatowitsch et al. 1999). Although the genetic status of the hybrid is still uncertain, populations examined so far are composed mostly of F1 hybrids (Kuehn et al. 1999, A.A. Snow, T. Fér, R. Wildova, and D.E. Goldberg, *unpublished data*). *Typha x glauca* appears to exhibit hybrid vigor: it is taller than either parent species, is tolerant of prolonged flooding, drainage, and salinity, and is often argued to be able to outcompete them (Smith 1987, Waters and Shay 1990, 1992, Galatowitsch et al. 1999). For field identification, we used the ratio leaf width:leaf length and spike gap length, which were selected by discriminant function analysis to have the best fit with genetically identified samples (by RAPD and microsatellite analysis) of the hybrid and the two parent species (A.A. Snow, T. Fér, R. Wildova, and D.E. Goldberg, *unpublished data*).

Coastal wetlands survey

Three Great Lakes coastal marshes in northern Michigan were chosen to quantify the relationships among *T. x glauca* invasion, nutrient availability, and the native community: Cheboygan marsh on Lake Huron (45°39’31’’N, 84°28’16’’W), Pt. la Barbe marsh in the Straits of Mackinac (45°50’20’’N, 84°45’24’’W), and Cecil Bay marsh on Lake Michigan (45°44’48’’N, 84°48’02’’W). Each site contained both an area of native vegetation and a considerable stand of *T. x glauca*.

In 2003, one transect was run through each marsh (ranging from 200-285 m), extending perpendicular to the shoreline. A 1 m^2 plot was set up approximately every 20 m along the transect. In each plot, stems of each species of vascular plant were counted (seedlings excluded) and percent cover of litter/standing dead was estimated. Some *T. angustifolia* was mixed in with the *T. x glauca* at all of the sites; *T. latifolia* was very rare at all the sites and not present in or near any of the transects. All other species in the plots were native, with a few exceptions present at low abundance and in fewer than 5% of the plots: *Poa compressa,* and possibly exotic genotypes of *Phalaris arundinacea* and *Phragmites australis*. Species richness of the native (non-*Typha*) species was tallied, and Shannon-Wiener diversity was calculated as $H = \sum(-p_i \ln p_i)$, where p_i is the proportion of total native stems of species *i*. For each plot, litter depth, soil temperature at 10 cm, and water depth were measured, and a single soil sample (10 cm depth) was collected. Great Lakes water levels are very dynamic so water depth measurements only indicate relative depths within a site. Soil samples were dried (70°C) and sieved (2 mm), and extractable PO_4^{3-}, NO_3^-, NH_4^+, and soil organic matter (SOM) were quantified using the analytical methods described below for the transplant experiment. Oven dried soil was used for this analysis; thus the results serve as a general index of relative amounts of inorganic soil N and P within and among the transects, but cannot be used for comparison with absolute amounts based on wet soil extraction in the following transplant experiment or other studies due to the transformations that occur during the drying process.

Statistical analyses. The sample size for each site was small (n=10, 12, 15), so data from the three sites were pooled and analyzed together (except for the species composition analysis described below). Because many of the environmental variables covaried, their relationships were investigated using principal components analysis (PCA) with Canoco 4.0 (ter Braak 1987, ter Braak and Smilauer 1998). Variables that appeared to be nonlinearly related were analyzed pairwise with quadratic regressions (SPSS 11).

Patterns between native species composition and the environmental variables (including *T. x glauca*) were tested using ordination methods with Canoco 4.0. Species stem densities were log-transformed to counteract skewness. Species present in fewer than 5% of the plots (doubletons and singletons) were omitted from the analysis, because they do not contribute greatly to species composition and standardization with only 2 occurrences can bias results. A preliminary detrended components analysis (DCA, Hill and Gauch (1980)) was performed to determine if linear or nonlinear (unimodal) methods were most appropriate. The length of the main floristic gradient in the DCA was 4.090 standard deviations, so a nonlinear canonical correspondence analysis (CCA) was chosen because nonlinear responses are expected along gradients of length > 4. In the CCA, site was used as a covariable. Due to the large number of environmental variables (8), forward selection was used to select only the variables that contributed significantly ($p<0.05$) to explaining variation in species composition with statistical testing by unrestricted Monte Carlo permutation tests for each added variable (ter Braak 1990, ter Braak and Verdonschot 1995). The unique contribution of each selected environmental variable was determined by performing a CCA with all other environmental variables and site as covariables; statistical significance of this was tested using Monte Carlo permutation tests within Canoco, with 499 permutations within site, and significance based on the overall (trace) statistic.

Transplant experiment

Study site / experimental design. The transplant experiment was conducted in Cheboygan marsh. The native vegetation at this site consists mainly of about 15 species of rushes (Juncaceae) and sedges (Cyperaceae) as well as a few species of wetland grasses and forbs. *Typha x glauca* is thought to have invaded the marsh 30-40 years ago and now occupies approximately 2/3 of the marsh area (N.C. Tuchman, P. Geddes, D. Larkin, R. Wildova, K.J. Jankowski, and D.E. Goldberg, *unpublished manuscript*).

In July 2004, live *T. x glauca* plants and *T. x glauca* litter were transplanted in a factorial design into 1 m^2 plots in 10 replicate blocks throughout the uninvaded area of the marsh. These four treatments will be referred to as the following: no live/no litter, litter only, live only, and live+litter. Live *T. x glauca* plants were collected from 10 locations, at least 20 m apart, throughout the dense *T. x glauca* stand to attempt to maximize genetic diversity, so that results can be better generalized to *T. x glauca* as a taxon. Because *T. x glauca* grows rapidly, only 10 stems (1/3 the density of the dense *T. x glauca* stand in the marsh) were planted per plot; by the next growing season when the data reported here were collected (2005), mean *T. x glauca* density had increased to 25 stems per m^2. Surface *T. x glauca* litter was collected at the same locations, mixed, and the equivalent of 2 kg dry weight (average aboveground litter in dense *T. x glauca* stands) was transplanted per plot. Litter was held in place from movement by water by pond netting (mesh size approx. 1 cm), which was kept on the litter plots throughout the duration of the experiment. *Typha* litter is typically a mass of senescent stems still rooted in place but bent horizontally and lying on the surface; thus, the net helps mimic this relative litter immobility; in general, free-floating litter and litter removal from the marsh due to water movement by seiches is highly uncommon (*personal observation*). At the end of the 2004 growing season, *T. x glauca* litter produced by the live only and the live+litter plots was clipped, divided equally, and placed under the netting in the litter only and live+litter plots.

Prior to transplanting, all treatment plots were clipped and cleared of native plants and native litter so that the stems of native plants would not be crushed in the litter treatment, potentially causing an influx of nutrients to the soil. For this reason, an additional control plot (a pretreatment clipping control) was also established in each block, to test the effects of clipping of all treatment plots. The amount of litter removed from native plots (190 g/m^2) was only about 10% of the amount of cattail litter added (2000 g/m^2), so it is unlikely that its removal had substantial impact on the results.

Environmental measurements. Available NH_4^+ and NO_3^- and net N mineralization measurements were taken in each plot in June and August 2005. N mineralization was measured using 1 month *in situ* buried bag incubations. On the first of each month, two soil cores (5 cm diameter x 10 cm depth) were taken from each plot and placed in a polyethylene bag; one bag was put on ice and transported back to the lab for processing, and the other was returned to the soil. Incubated samples were retrieved from the field after 28 days. In the lab, soils were immediately sieved (2 mm) and a 10 g subsample was extracted for 1 hour with 40 ml 2 M KCl. Extracts were filtered

(Whatman GF/F) and frozen until colorimetric analysis for NH_4^+ and NO_3^- with a Bran Luebbe autoanalyzer 3 (Eaton et al. 1995). A 10 g subsample was dried at 105°C for wet:dry ratio, and SOM was measured by combusting the dried sample for 5 hours at 500°C. Bulk density (g soil ml^{-1}) in each plot was determined by subtracting the mass and volume of the coarse fraction from the total core mass and volume for the June incubated soil cores. There were only slight block differences in bulk density, so available nutrients and mineralization rates were calculated on an aerial basis using the overall average bulk density (1.34 g ml^{-1}). Nitrate concentrations for all initial samples were zero or negligible, as is often the case in anaerobic wetland soils (Bowden 1987), so NH_4^+-N (mg N m^{-2}) in initial soil cores was used as a measure of available N. N mineralization (mg N $m^{-2}d^{-1}$) was calculated as the increase in NH_4^+-N plus NO_3^--N over the 28 days.

Available phosphorus was measured in August 2005 by extracting a 10 g subsample from the August initial soil core with 40 ml Troug's solution (1 mM H_2SO_4+$(NH_4)_2SO_4$ pH 3) for 1 hour. The extract was centrifuged, filtered (0.45μm), and refrigerated (4°C) until colorimetric analysis on a Bran Luebbe autoanalyzer 3 (Eaton et al. 1995).

Light penetration through the vegetation and litter was measured in late July 2005 as photon flux (μmol $s^{-1}m^{-2}$) at the soil surface divided by total photon flux above the vegetation using a LI-COR quantum sensor LI-250A. Light at the soil surface was measured at a point location by averaging over a 15 second period. Two point locations were measured per plot and these two measurements were averaged. All measurements were taken within one hour of solar noon.

Water depth and soil temperature (5 cm below the surface) was measured in each plot twice in June and twice in August. Temperature measurements were taken within a 1.5 hour block of time starting about 45 minutes after solar noon because after that soil temperature no longer warms substantially. The water and temperature measurements were averaged by month.

Plant measurements. Plant community composition in the four factorial experimental treatments was quantified in mid July 2005 by stem counts of rooted vascular plants. Shannon-Weiner diversity (H) was calculated for each plot using stem densities of native species, as above in the survey. Similar to the survey, almost all species observed during the experiment (other than the transplanted *T. x glauca*) were native. Exceptions included *Agrostis gigantea* (common) and possible exotic genotypes of *Agrostis stolonifera* and *Phalaris arundinacea* (both present in fewer than 5% of plots). The maximum height of the native vegetation and of *T. x glauca* was measured in all plots in late July 2005.

The control plots for the pretreatment clipping were not censused for stem densities due to time constraints; because the majority of the species are clonal and resprout from rhizomes, clipping is not likely to have a large effect on species richness and relative abundance.

Statistical analysis. The effect of treatment (live, litter, and live x litter interaction) and block on available NH_4^+ and N mineralization was analyzed with repeated-measures ANOVA (SPSS 11) because data were taken in both June and August. Treatment and block effects on soil variables that were measured once (PO_4^{3-}, SOM, light) and the native community measurements (stem density, species diversity, native vegetation max height) were analyzed with ANOVA (SPSS 11). Interaction terms including blocks in the ANOVAs were not investigated due to limited degrees of freedom (n=10 per treatment combination), and because blocks did not appear to respond qualitatively differently to the different treatments.

The effect of pretreatment clipping was analyzed with a separate repeated-measures or regular ANOVA in which the no-litter/no-live treatment plot (the control for the factorial experiment) was compared to the pretreatment clipping control plot.

The effect of the experimental treatments on species composition of non-*Typha* spp. was analyzed using Canoco 4.0. Methods were identical to those used for the field survey CCA with the following exceptions: 1. forward selection was not used because there were only three treatment variables, and 2. block was used as a covariable. In general, in doing a CCA, species abundances are standardized by species and by plot, which converts abundances to relative abundances. Thus, CCA tests whether species relative abundances are differentially affected by the treatments.

To determine whether experimental results were similar to field observations, the species responses to litter from the 2005 transplant experiment were compared to those from the 2003 survey. The Pearson correlation coefficient was calculated and a one-tailed significance test was done to determine if species scores along the litter axis from the survey CCA ordination were positively correlated with those from the experiment ordination.

Results

Coastal wetlands survey

The environmental variables indicative of high nutrient conditions and low light (NH_4^+, PO_4^{3-}, SOM, litter depth, litter percent cover, soil temperature) covaried strongly with each other as reflected in axis 1 in the PCA (Fig. 2.2). Axis 1 explains 60.8% of the variance in environmental variables. Water depth varied only with axis 2, which explains 15.1% of the variance, thus it was not correlated with any of the above variables (Fig. 2.2).

Live *T. x glauca* density was associated with high nutrients (NH_4^+, PO_4^{3-}, SOM) and low light environments (high litter depth, litter percent cover, low soil temperature) because it also loaded positively on axis 1 of the PCA (Fig. 2.2). It was not related to water depth (Fig. 2.2). Interestingly, despite the overall positive correlations between *T. x glauca* density and high nutrients, *T. x glauca* stems were not restricted to high nutrient locations; rather they were also present in low nutrient microsites and were also abundant in one of the sites which was fairly oligotrophic overall (Fig. 2.3).

The stem density of the native community was negatively associated with *T. x glauca* density, litter depth, and the covarying environmental variables (NH_4^+, PO_4^{3-}, SOM, litter % cover, soil temperature), because it loaded negatively on axis 1 of the PCA (Fig. 2.2). Shannon-Weiner diversity was negatively associated with litter percent cover and water depth on the PCA but was not associated with live *T. x glauca* density or any of the other environmental variables as shown by their orthogonal vectors in the PCA (Fig. 2.2). However, diversity was strongly related nonlinearly to litter depth ($R^2=0.557$, $p<0.001$), in a hump-shaped relationship with highest diversity at intermediate litter depths (Fig. 2.4). Weaker nonlinear (hump-shaped) relationships were also found between diversity and soil NH_4^+ (R^2=0.237, p=0.010) and SOM (R^2=0.228, p=0.012) (Fig. 2.4). Interestingly, diversity was not non-linearly related to *T. x glauca* stem density (R^2=0.014, p=0.79). Species richness showed correlation patterns similar to Shannon-Weiner diversity (data not shown).

The results from forward selection in the CCA indicate that four of the eight environmental variables explain a significant and substantial (28.0%) portion of the variance in species composition: soil temperature, water depth, litter depth, and PO_4^{3-} (Fig. 2.5). Notably, density of live *T. x glauca* stems was not in this group. Site effects (differences among the three marshes) explained 14.2% of the variance. The first axis (13.9% of the variance) is a gradient of increasing litter and nutrient levels and decreasing light levels. Many of the rush (Juncaceae) and sedge, bulrush, and spikerush (Cyperaceae) species that are typical wetland dominants were more common at the low litter/low nutrient/high light end of the gradient, including *Juncus* spp., *Eleocharis* spp., *Schoenoplectus* spp., and *Carex viridula*. Grasses and forbs predominate at the high litter/high nutrient/low light end of the gradient, with the exception of four *Carex* species (Cyperaceae), which were positively associated with this axis. These species are all fairly productive and generate a lot of litter themselves.

Transplant experiment

Effects of* T. x glauca *on the abiotic environment. All significant treatment effects on the abiotic environment were brought about by litter, and not by the live *T. x glauca* transplants (Table 2.1, Fig. 2.6). Addition of *T. x glauca* litter increased extractable soil NH_4^+ and N mineralization rates in both June and August measurement periods. N mineralization was higher overall in June than August (time effect) and was more affected by litter in June (time*litter effect, F=6.533, p=0.017). However, neither litter nor live *T. x glauca* affected soil extractable PO_4^{3-} or SOM (Table 2.1, Fig. 2.6).

Light penetrating to the soil surface was very significantly reduced by litter, from 70% of full sunlight in no litter/no *Typha* plots to 1% in litter plots (Table 2.1, Fig. 2.6). Light was not affected by live *Typha*.

Effects of* T. x glauca *on the plant community. As with effects on the abiotic environment, all significant plant community effects were brought about by the litter treatment, not by live *T. x glauca* (Table 2.1). Litter somewhat reduced species diversity and dramatically reduced total stem density by almost 75% compared to the no litter plots (Table 2.1, Fig. 2.7). This was true at the species level as well; for 23 out of the 26 species (doubletons and singletons excluded) litter reduced stem densities by 32-100%. Only three forbs increased in absolute abundance with the litter treatment. In contrast, the presence of litter resulted in taller native vegetation by an average of 8 cm compared to no litter treatment plots (Fig. 2.7).

CCA ordination of species composition and post hoc tests showed that *Typha* litter, but not live *Typha* or the interaction, significantly affected the plant community (Fig. 2.8). Despite overall reduction in stem density by litter, species varied in their extent of depression by litter (Fig. 2.8). A few of the dominant and common wetland species increased slightly in relative abundance (*Schoenoplectus americanus*, *Juncus balticus*, and *Carex aquatilis*) or were unaffected (*Eleocharis smallii*, *E. erythropoda, J. nodosus*, *S. validus*, and *S. acutus*) by litter addition. However, ten species were relatively negatively affected by litter, including the common species *J. alpinus*, *J. articulatus, C. viridula, C. hystericina,* and *E. pauciflora*.

We compared species responses to litter from the 2005 transplant experiment to the 2003 survey to assess whether the litter treatment produced realistic community consequences. The species scores along the litter axis from the survey ordination (CCA) were positively correlated with those from experiment ordination (r=0.409, p=0.046, n=18, one outlier was removed). Thus, species that were more positively associated with litter in the survey were also more positively associated with litter in the experiment.

Effects of* T. x glauca *litter on* T. x glauca *growth. Litter did not affect the density of *T. x glauca* stems, with 23.8 ± 3.1 vs. 26.8 ± 1.2 stems in the no litter vs. litter treatments (Table 2.1). However, *T. x glauca* stems grew taller when grown in the litter plots: their maximum height increased by 18.5 cm (Table 2.1, Fig. 2.9).

Spatial heterogeneity and block effects. Significant block effects in almost all of the analyses (Table 2.1) indicate considerable spatial heterogeneity in both the environmental properties and the plant community. This is not surprising because the blocks were intentionally situated over a 0.5 km stretch of the marsh, to test the effect of *T. x glauca* in a variety of different abiotic environments and plant assemblages. However, most heterogeneity in nutrient properties (NH_4^+, N mineralization, PO_4^{3-}, and SOM) was due to one block that had high clay content and higher elevation (no standing water) compared to other blocks. Excluding this block from the analyses eliminated or weakened block effects without greatly changing litter treatment effects on soil nutrient properties. Heterogeneity in native species density and diversity among the blocks was driven by water depth. When water depth was added as a covariate to the ANOVAs, block effects became non-significant or weaker, again without greatly changing the effect of the litter treatment. Heterogeneity in native vegetation maximum height was due to a block dominated by the tall *Schoenoplectus acutus*; excluding this block from the analysis removed block effects, while litter remained significant. Overall, much of the heterogeneity in environmental and plant community variables was explained by other variables that were measured in this study or by taking single “outlier” blocks out of the analysis. Nevertheless, including covariates or excluding outliers did not change the strong effects of the litter treatment and the lack of effect of the live treatment.

Controls for pretreatment clipping. Because all experimental plots were clipped prior to treatment, we compared an additional control plot (clipping control) to the no live/no litter (treatment control) plot to assess the effect of this pretreatment clipping on the environment and plant community. Most environmental and plant measurements were unaffected by this initial clipping, except for light, stem density, and native plant height. The no live/no litter treatment plots had significantly more light penetration (70%) compared to the clipping control plots (39%, $F_{1,9}$=36.19, p<0.001). Although we did not measure stem density in the clipping control plots, it appeared to be reduced substantially in the no live/no litter treatment plots by approximately 50%. The lower stem density and more light in the clipped experimental plots is not surprising, because they had not grown back to full cover nor had substantial native litter accumulated after only one growing season. Despite this significant effect of clipping, the treatment effects of *Typha* litter on these two variables were so dramatic that results would not change qualitatively if plots were not clipped. Also, the native vegetation was shorter by 20% in the no live/no litter treatment control than in the clipping control plots ($F_{1,9}$=20.46, p=0.001), however *Typha* litter effects on this variable were also small (an increase of 10%).

Discussion

Elevated nutrients – invasion – native species loss

The association of elevated nutrients, invasion, and native species loss is common in many wetland systems with many different wetland invaders, including *Phragmites australis*, *Phalaris arundinacea*, and *Typha domingensis* (Galatowitsch et al. 1999, Meyerson et al. 2000, Childers et al. 2003, Kercher et al. 2007). Our results from the survey of *T. x glauca* invasion are also consistent with this association, but only if the relationship is mediated by litter. *Typha x glauca* density was positively associated with high soil nutrients; however, native diversity and species composition were related only to litter and nutrient levels, not invader stem density. The positive association between *T. x glauca* density and deep litter and the observation that most of the deep litter in the marsh is from *Typha*, suggests that *T. x glauca* affects native species non-trophically through litter production.

We tested these non-trophic interactions, as well as competition and invader-directed environmental change, with a transplant experiment, in order to begin to assess some of the possible causal pathways linking elevated nutrients, invasion, and native species loss (Fig. 2.1). The results suggest that invaders can drive environmental change, because transplanted *T. x glauca* litter increased soil NH_4^+ and rates of N mineralization. No evidence was found for resource competition between live *T. x glauca* and the native plant community; however, non-trophic effects were apparent because *T. x glauca* litter decreased light and decreased native plant density and diversity and altered community composition by decreasing relative abundances of common wetland rushes and sedges. These results suggest that invaders can drive environmental change once they reach a new habitat. The survey, as well as results from N.C. Tuchman, P. Geddes, D. Larkin, R. Wildova, K.J. Jankowski, and D.E. Goldberg (*unpublished manuscript*), indicates that *T. x glauca* is able to disperse to and establish in oligotrophic marshes and microhabitats. Therefore, model 5 is a potential pathway that may explain elevated nutrients, invasion, and native species decline in this system (Fig. 2.1). Model 3 may occur as well, as anthropogenic inputs have been demonstrated in some invaded systems (Davis and Ogden 1994, Drexler and Bedford 2002).

Many of the worst wetland invaders in N. America, *Phragmites australis*, *Phalaris arundinacea*, *Typha domingensis*, and *T. angustifolia* share characteristics with *T. x glauca*, such as tall stature, fast growth rate, clonality, and litter production and accumulation. Thus, it is plausible that the mechanisms behind *T. x glauca's* association with elevated soil nutrients (litter production/decomposition) and low species diversity (litter accumulation/light reduction) may be applicable to the other wetland invaders as well. Interestingly, *Lythrum salicaria* is a notable exception, with highly decomposable leaves leading to little litter accumulation (Emery and Perry 1996); therefore changes in diversity associated with *Lythrum* invasion may not be mediated through litter. Below, we discuss the two components, nutrient increase and native decline, of the invader-directed pathway supported by this study (model 5) and their implications both for this system and for wetland invaders more broadly.

Mechanisms behind invader-directed nutrient increase

Wetland invaders are commonly associated with increased nitrogen cycling (Ehrenfeld 2003), which has been attributed to oxygen release by the invader (*Phragmites australis*) (Windham and Lathrop 1999, Windham and Ehrenfeld 2003), oxygen and exudate release (*Phalaris arundinacea*) (Edwards et al. 2006), and SOM quality and quantity (*Lythrum salicaria*) (Fickbohm and Zhu 2006). Studies in upland systems have also found that invasives are often associated with increased soil nitrogen mineralization due to their higher litter quality or quantity (Ehrenfeld 2003). However, all of these previous studies (with the single exception of the constructed wetland of Edwards et al. (2006)) are correlative and the mechanism actually causing the effect was not experimentally manipulated or measured.

Consistent with previous reports, our survey data indicated that soil nutrients (NH_4^+, PO_4^{3-}, SOM), *T. x glauca* density, and litter depth were all positively correlated. The experiment suggests that the mechanism underlying this pattern could be the high litter production of the invader, which in turn increases extractable N and N mineralization rates, rather than any effect of live plants. While the experimental addition of litter did not result in significant increases in SOM and PO_4^{3-} within a year after deposition, such effects may well appear over the long term as the litter is further decomposed and incorporated into the soil (Schlesinger 1997, Bridgham et al. 1998).

The rapidity with which the litter addition treatment increased extractable N and mineralization rate might seem surprising because most litter bag studies see an initial period of immobilization rather than mineralization after deposition (Schlesinger 1997, Windham and Ehrenfeld 2003). However, these studies follow immobilization in the litter itself rather than in the underlying soil, as we did in this study. We hypothesize that the *T. x glauca* litter may be leaching labile organic compounds to the pore water of the sediments below. Consistent with this hypothesis, preliminary sampling of pore water showed that litter plots had significantly higher dissolved organic carbon and total dissolved nitrogen (but not dissolved organic nitrogen) compared to plots without litter (and live *T. x glauca* had no effect) (Farrer, *unpublished data*); however more extensive sampling is necessary. This short term positive effect of litter addition on nutrient cycling rates has not been observed in forest manipulations (Holub et al. 2005), but it may be more common in wetlands because standing water tends to accelerate fragmentation, decomposition, and transport of litter leachate to the soil (Welsch and Yavitt 2003). Although this leaching process may be short-term, each season the addition of fresh litter as *Typha* plants senesce will provide the soil with leachate; thus this mechanism of nutrient increase may be particularly important in early stages of invasion.

Long-term litter dynamics may also lead to increases in soil nutrient availability. *Typha* and other wetland invasives are highly productive, generating large quantities of litter which are large stores of organic N. We suggest that *Typha* litter will also increase soil nutrient availability in the long term through the release of the N from the litter via mineralization and through its incorporation into SOM, which is an N source and increases cation exchange capacity.

Interestingly, live *T. x glauca* plants do not affect nutrient cycling or nutrient pools, even though stem densities in experimental plots are similar to those found in *T. x glauca* monocultures in the field. Therefore, neither resource depletion due to uptake nor facilitation of N cycling due to oxygenation or root exudates (Windham and Lathrop 1999, Windham and Ehrenfeld 2003, Edwards et al. 2006) appears to be important in this system.

Mechanisms behind decline in native species

Live *T. x glauca* plants in the experiment do not affect native species density, diversity, or species composition. Moreover, neither nutrients nor light is reduced by live plants, suggesting that resource competition (i.e. column 2, Fig. 2.1) is not a likely mechanism of native species decline in this system. Light limitation is commonly thought to be important in native species decline in wetlands either because the invader is taller than the natives (Lenssen et al. 2000, Drexler and Bedford 2002, Woo and Zedler 2002) or because of the growth/allocation behavior of the native plants when grown with the invader (Green and Galatowitsch 2002, Minchinton and Bertness 2003). In most studies, however, light levels are not measured, and because light reduction also depends on leaf arrangement and orientation as well as stem density, height comparisons alone are insufficient to infer light limitation (Güsewell and Edwards 1999).

In contrast, non-trophic effects through litter (column 3, Fig. 2.1) seem to be the primary mechanism of reduction in native density and diversity and changes in species composition. Non-trophic effects of invasive plants are not considered by most invasive species studies, despite litter being recognized as an important factor in structuring native plant communities (Facelli and Pickett 1991, Xiong and Nilsson 1999). Only two previous field experiments on invasive species (*T. angustifolia* and *Phragmites australis*) have manipulated litter independently of live plants (Hager 2004, Minchinton et al.

2006). Our results and the results of both previous studies suggest that suppression of growth is at least as strong by litter as by live plants. Negative effects of litter on plant establishment and growth is likely due either to light reduction (98% in our study) and/or to physical obstruction of growth (Lenssen et al. 2000).

Positive feedbacks

When a plant affects environmental conditions, these effects are likely to feedback to influence the performance of that plant (Bever et al. 1997, Van Breemen and Finzi 1998, Ehrenfeld et al. 2005). A feedback is positive if a plant modifies the environment in a way that benefits itself, by increasing its population or individual growth (Ehrenfeld et al. 2005). Positive feedbacks may be a very effective mechanism of invasion (Ehrenfeld 2003, Levine et al. 2006); and positive feedbacks through nutrient dynamics have been hypothesized as a mechanism of invasion for *Berberis thunbergii* and *Microstegium vimineum* in deciduous forests (Ehrenfeld et al. 2001), *Bromus tectorum* invasion in arid grasslands (Sperry et al. 2006), as well as a number of invaders in Hawaii (Allison and Vitousek 2004).

Feedbacks can be incorporated into the framework of models presented in Fig. 2.1. When the invader affects the environment, this influences native species, as shown by the arrow from the environment to the natives. However, this environmental change also affects the invader's own growth; therefore an arrow should also point from the environment back to the invader (this was not included in Fig. 2.1 for simplicity). The results from this study suggest that *T. x glauca* may produce a positive feedback through its litter. Although *Typha* litter had no effect on *T. x glauca* stem density, it significantly increased the growth of individual *T. x glauca* stems, possibly due to the increased N under the litter. Thus, high litter production by *T. x glauca* seems to create a high nutrient/low light environment which benefits itself.

The low light under large amounts of litter does not negatively affect *T. x glauca* probably due to its large rhizomes compared to native species, which provide substantial energy reserves allowing new shoots to quickly grow through the shaded litter layer. Also, *T. x glauca* stems have a large diameter and are relatively stiff when young, so new shoots would be able to push through the obstructing litter layer to reach the light. Once stems penetrate the litter layer, they can take advantage of the elevated N.

Implications

This study demonstrates that invaders can increase nutrients in wetlands and therefore act as the driver of environmental change, and that nontrophic effects can have much stronger negative effects on native plants than competition for resources. Thus, model 5 (Fig. 2.1) very likely contributes to *T. x glauca* invasion. Nevertheless, human-directed eutrophication could also play a role in *T. x glauca* invasions (i.e., model 3); the models are not mutually exclusive. Regardless of the source, increased nutrients would promote invasion due to the rapid and positive response of *T. x glauca* (Woo and Zedler 2002), which would in turn promote litter production and suppression of native species. Anthropogenic nutrient input may, in fact, be important in initiating the positive feedback loop by *T. x glauca* and speed the spread of the invader though the site. However, our results suggest that the decline in native species will occur only after litter builds up, via nontrophic effects.

While anthropogenic nutrient input probably can and does promote invasion by *T. x glauca* and consequent local diversity decline, the results from this study indicate that it is not necessary: *T. x glauca* can produce a high nutrient, low density/diversity wetland community all by itself. This has very different management and remediation implications than a purely human-directed invasion. For example, it indicates that a cessation of anthropogenic nutrient loading, although it may slow the process, will not prevent *T. x glauca* from expanding, elevating nutrient levels, and decreasing the diversity in wetlands. Because transplants grew well even in the low nutrient marsh conditions (in the no-litter plots) and because of the ability of *T. x glauca* to invade oligotrophic sites (this study, and N.C. Tuchman, P. Geddes, D. Larkin, R. Wildova, K.J. Jankowski, and D.E. Goldberg, *unpublished manuscript*) even pristine wetlands, removed from anthropogenic influence, are at risk of invasion. Because of the many environmental impacts of *T. x glauca*, the removal of the living *T. x glauca* plants will not restore wetlands; nutrients will still be elevated in the soil, rhizomes and aboveground litter will continue to contribute to elevated N mineralization, and any remaining litter will still suppress native plant growth. Moreover, if only live *T. x glauca* is removed from a site, the remaining environmental conditions may make re-invasion much more likely.

The similarities in morphology, growth response, and litter production between *T. x glauca* and other large, clonal wetland invaders like *Phragmites*, *Phalaris*, and other *Typha* species suggest that the mechanisms behind nutrient increase and native species decline found in this study may be more broadly applicable.

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Table 2.1. Effect of litter and live *T. x glauca* treatments on environmental and community characteristics. Data shown are F-statistics from ANOVAs with significance indicated by asterisks (***p<0.001, **p<0.01, *p<0.05). NH_4^+ and N mineralization were measured in June and August and tested with repeated measures ANOVA. Interactions of the treatments and block with time are not shown, but are mentioned in the text if significant. All other variables were tested with ANOVA.

Variable	Error df	Litter (df=1)	Live *Typha* (df=1)	Litter x Live (df=1)	Block (df=9)	Time (df=1)
NH_4^+	27	7.13*	0.29	1.56	3.36**	0.282
N mineralization	27	59.66***	0.67	0.85	5.79***	41.72***
PO_4^{3-}	27	2.06	0.07	0.68	4.30**	--
SOM	27	1.70	0.34	1.29	5.27***	--
Light	27	426.15***	1.59	1.54	1.33	--
Stem density	27	20.96***	0.70	0.09	4.08**	--
Species diversity	27	4.69*	0.65	0.54	6.48***	--
Native vegetation max height	27	5.30*	1.41	2.15	11.97***	--
Typha density	9	0.85	--	--	1.05	--
Typha max height	9	16.19**	--	--	1.17	--

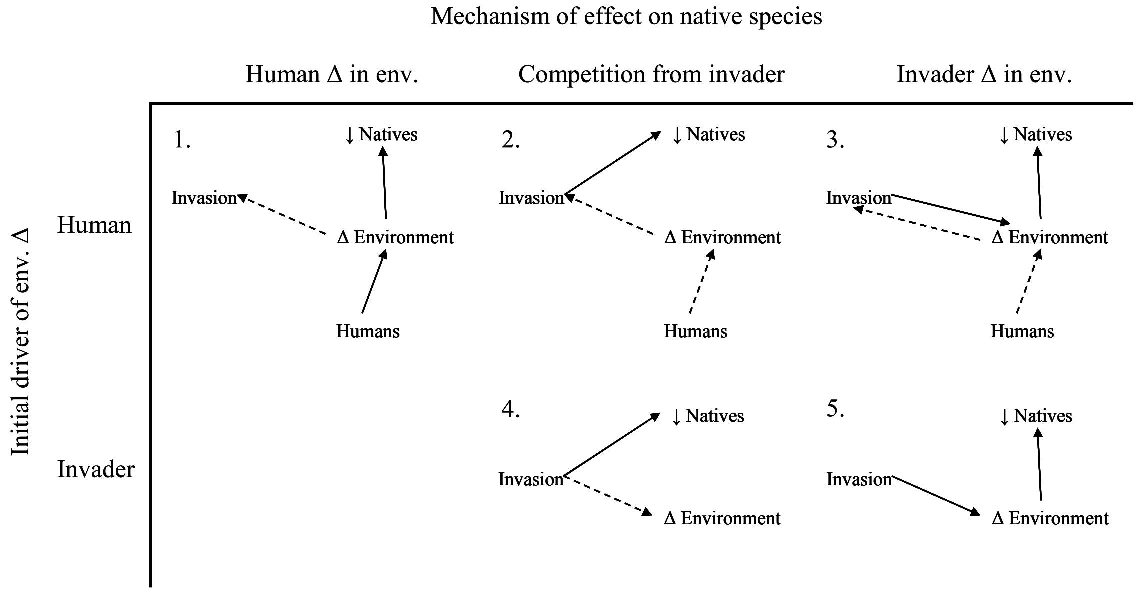


Fig. 2.1. Five models of causal relationships explaining the common pattern of invasion, environmental change, and decline in native species. The models are organized based on the initial driver of environmental change (left axis), and the mechanism of effect on native species (top axis). Either humans (models 1-3) or the invader (models 4-5) is the initial driver of the environmental change. Native species decline due to human changes in environment (model 1), resource competition from the invader (models 2, 4), or invader changes in the environment (non-trophic effects of the invader, models 3, 5). The solid lines indicate the pathway of native species decline, while the dashed lines represent concomitant changes with no direct effect on native species. None of the models are mutually exclusive and multiple causal pathways could contribute to the observed field pattern.

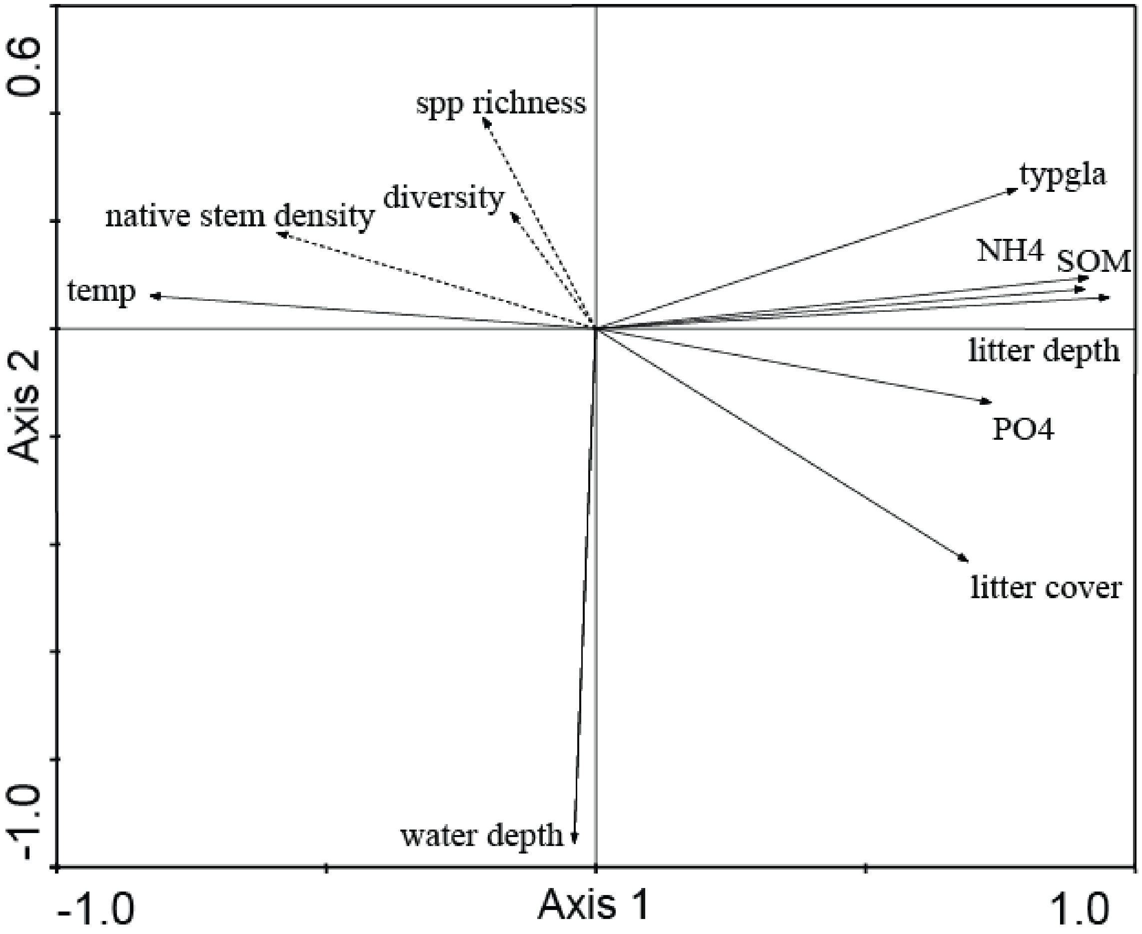


Fig. 2.2. Principle components analysis (PCA) ordination of environmental variables (solid lines) including *T. x glauca* density (typgla) from the field survey. Native stem density, species richness, and diversity were added as supplementary variables (dashed lines), so that they do not influence the ordination, but so that their correlations with the environmental variables can be visualized. Axis 1 explains 60.8% of all variation in environmental variables, axis 2 explains an additional 15.1%.

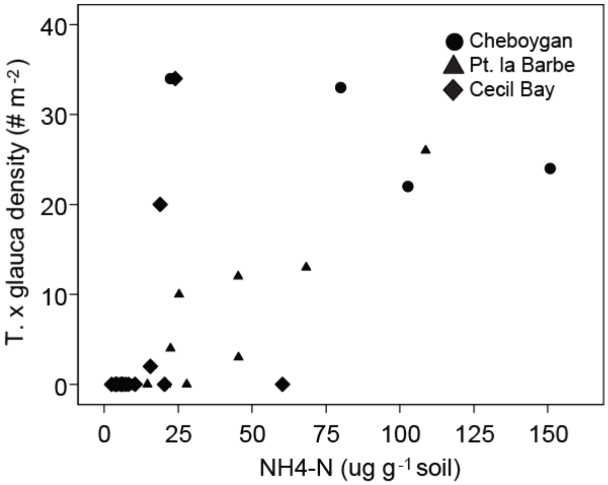


Fig. 2.3. *Typha x glauca* density and extractable nitrogen levels in the field survey. Note that *T. x glauca* is not restricted to high nutrient microsites and is abundant even in a site which is fairly oligotrophic overall (Cecil Bay).

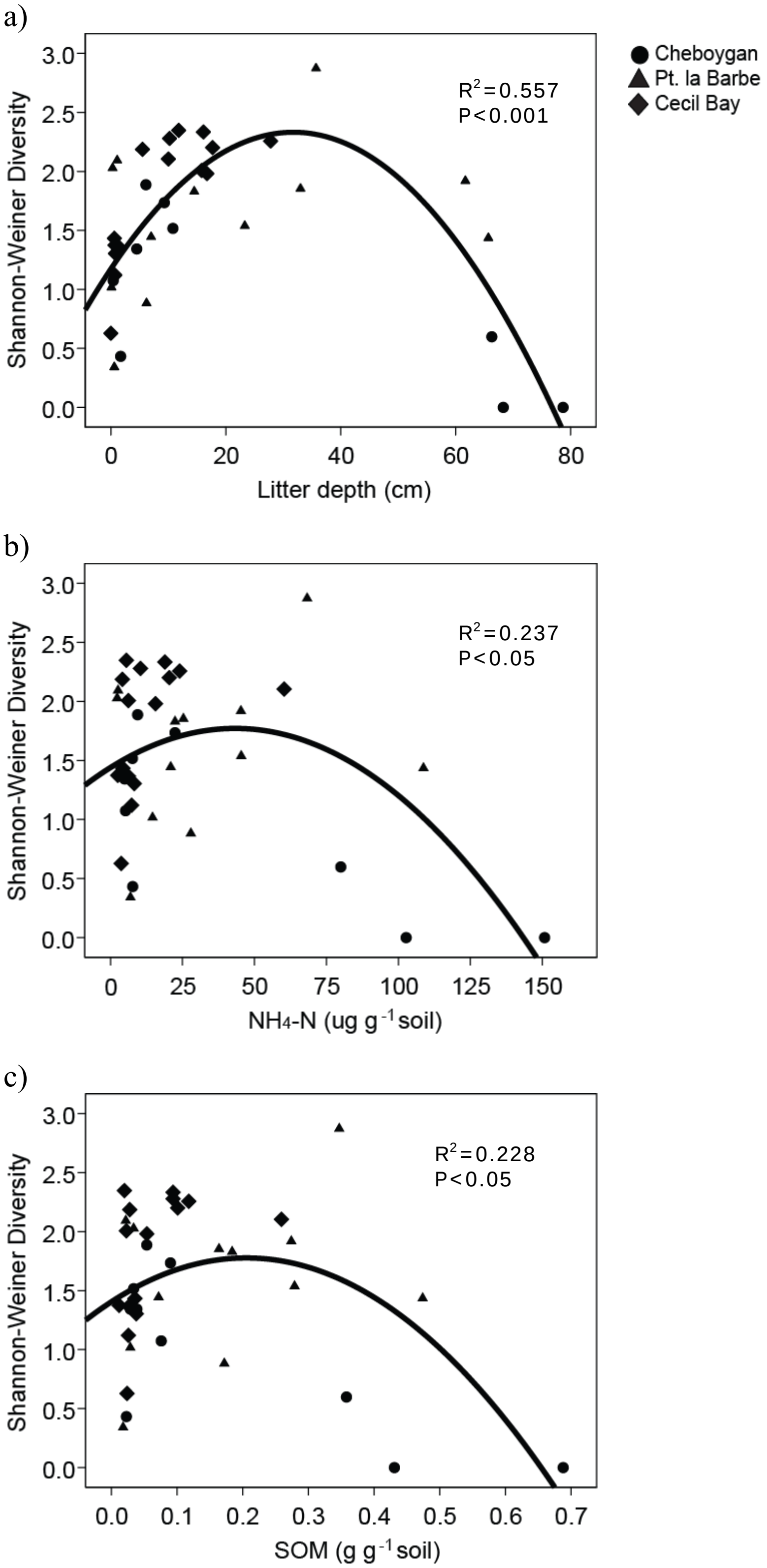


Fig. 2.4. Significant non-linear relationships between Shannon-Weiner diversity and environmental variables in the field survey.

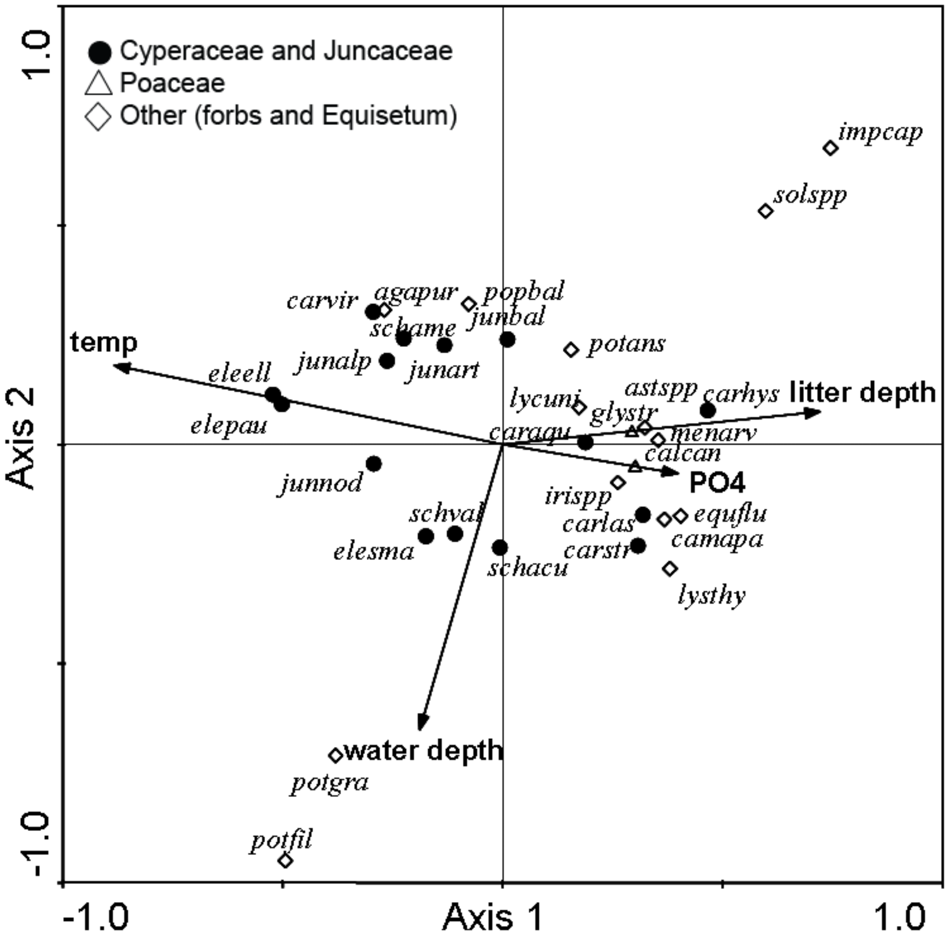
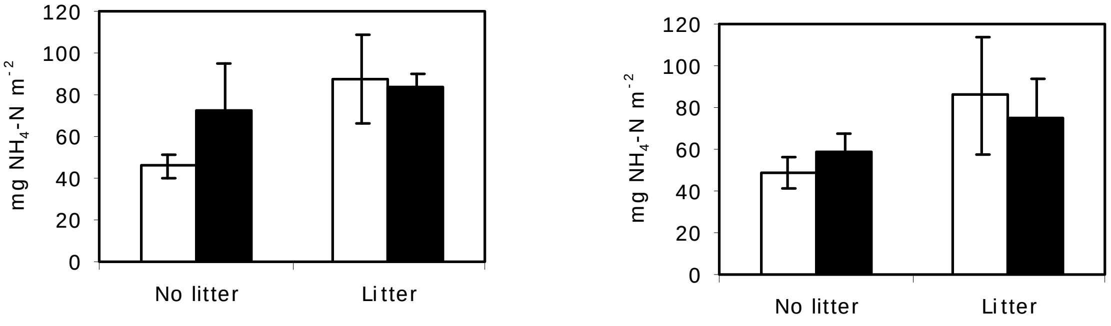
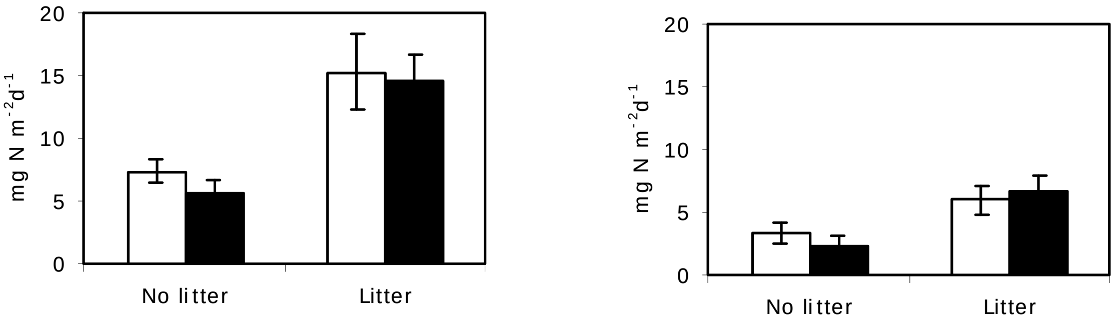


Fig. 2.5. Biplot of environmental variables and species scores from the canonical correspondence analysis (CCA) ordination of native species densities from the field survey. Axes 1 and 2 explain 13.9% and 8.4% of the total variation, respectively. The four environmental variables together explain 28.0% of the total floristic variation, and site explains 14.2%. Significant environmental variables were temperature (8.7% of the floristic variation), water depth (8.0%), litter depth (4.0%), and PO4 (2.9%); non significant variables were live *T. x glauca* density, litter % cover, NH4, and SOM. The most important (in fit and weight) 31 of 45 species are shown in the graph below. Abbreviations for species names are the first 3 letters of the genus and species: agapur=*Agalinis purpurea*, astspp=*Aster spp.*, calcan=*Calamagrostis canadensis*, camapa=*Campanula aparinoides*, caraqu=*Carex aquatilis*, carhys=*Carex hystericina*, carlas=*Carex lasiocarpa*, carstr=*Carex stricta*, carver=*Carex viridula*, eleell=*Eleocharis elliptica*, elepau=*Eleocharis pauciflora*, elesma=*Eleocharis smallii*, equflu=*Equisetum fluviatile*, glystr=*Glyceria striata*, Impcap=*Impatiens capensis*, irispp=*Iris spp.*, junalp=*Juncus alpinus*, junart=*Juncus articulatus*, junbal=*Juncus balticus*, junnod=*Juncus nodosus*, lycuni=*Lycopus uniflorus*, lysthy=*Lysimachia thyrsiflora*, menarv=*Mentha arvensis*, popbal=*Populus balsamifera*, potfil=*Potamogeton filiformis*, potgra=*Potamogeton gramineus*, potans=*Potentilla anserina*, schacu=*Schoenoplectus acutus*, schame=*Schoenoplectus americanus*, schval=*Schoenoplectus validus*, solspp=*Solidago spp.*



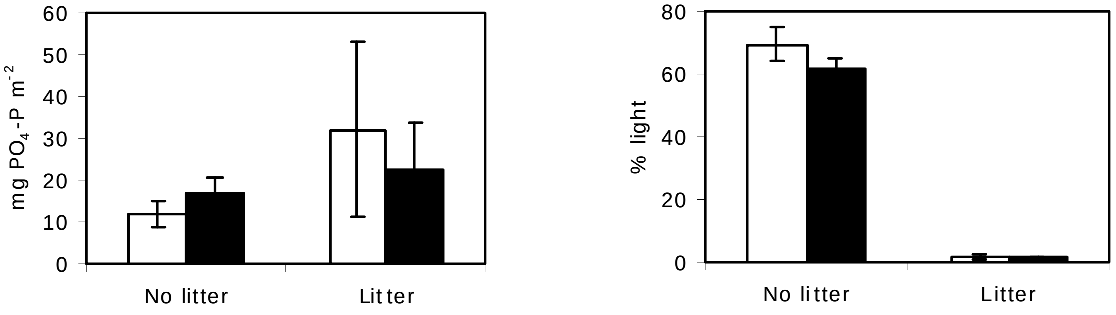
a) June NH_4^+

b) August NH_4^+



c) June N mineralization

d) August N mineralization



e) PO_4^{3-}

f) % of full sunlight

g) SOM

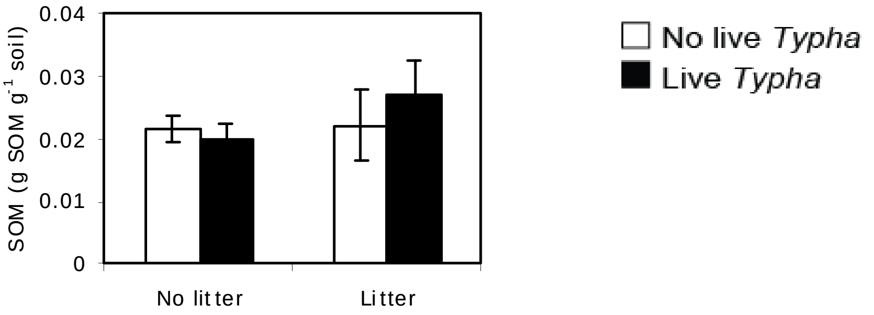


Fig. 2.6. Effect of transplanted *T. x glauca* plants and litter on soil NH_4^+ pools in June (a) and August (b), N mineralization in June (c) and August (d), soil PO_4^{3-} pools (e), light (f), and SOM (g). Numbers are means +/- SE (n=10). For ANOVA results see Table 2.1.

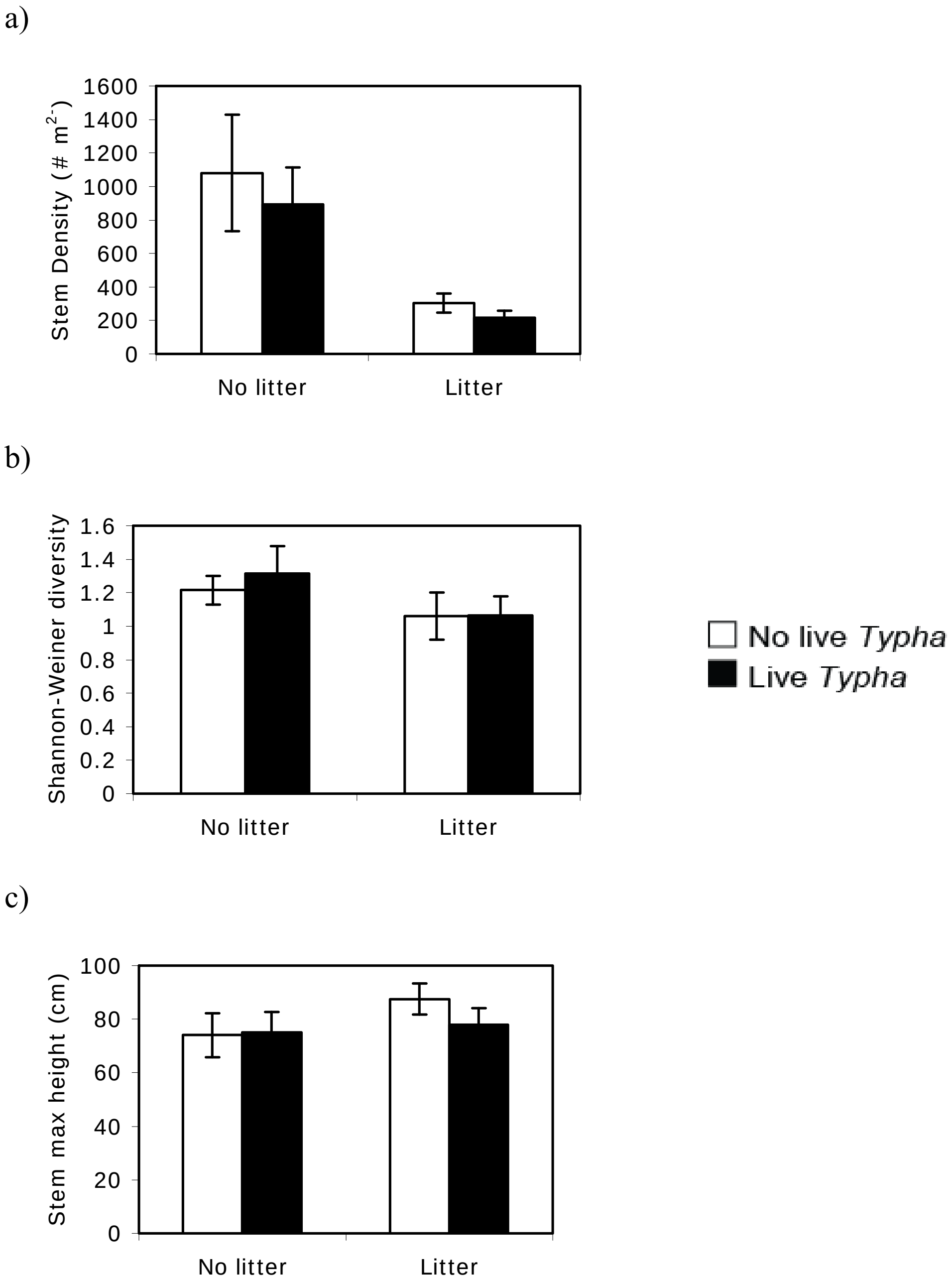


Fig. 2.7. Effect of transplanted *T. x glauca* plants and litter on stem density (a), species diversity (b), and maximum stem height (c) of the native vegetation (mean +/- SE, n=10). For ANOVA results see Table 2.1.

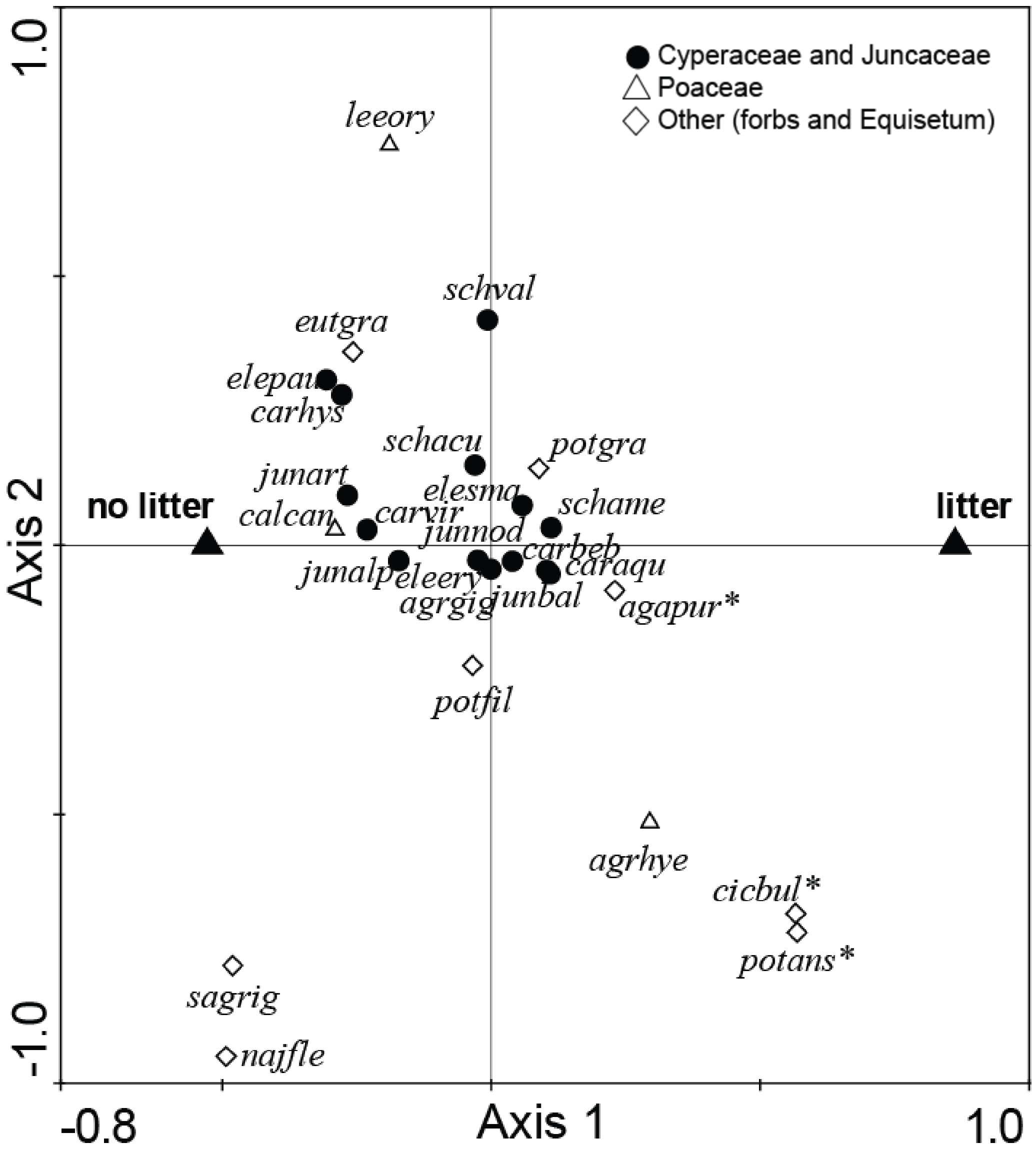


Fig. 2.8. Biplot of treatments and species scores from the CCA ordination of native species relative densities in the experimental plots. All 26 species are shown. Species with asterisks showed an increase in absolute abundance with the litter treatment as well as relative abundance. Axes 1 and 2 explain 3.0% and 6.0% of the total floristic variation, respectively. All treatment variables (litter, live, litter x live) together explained 4.5% of the floristic variation, while block explained 67.5%. Litter was the only treatment that explained a significant amount of the floristic variation by itself (3.0%); live *T. x glauca* and live x litter interaction had no significant effect on species composition. Abbreviations for species names are as in Fig. 2.5 with the following additions: agrgig=*Agrostis gigantea*, agrhye=*Agrostis hyemalis*, carbeb=*Carex bebbii*, cicbul=*Cicuta bulbifera*, eleery=*Eleocharis erythropoda*, eutgra=*Euthamia graminifolia*, leeory=*Leersia oryzoides*, najfle=*Najas flexilis*, sagrig=*Sagittaria rigida*.

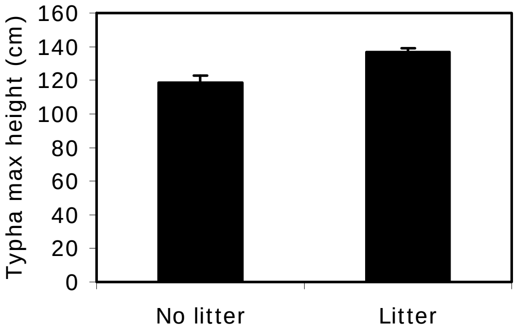


Fig. 2.9. Maximum height of *T. x glauca* transplants in no litter and litter addition plots (means +/- SE, n=10). For ANOVA results see Table 2.1.

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CHAPTER III

Time lags and the balance of positive and negative interactions in driving grassland community dynamics

Abstract

Both facilitative and competitive interactions occur simultaneously among plants, and the net balance between them can vary over time. Despite this, recent model-fitting studies have found that negative interactions predominate. This suggests that more complex models may be necessary to uncover facilitation. Here we fit models including seasonality, interannual variation, and time lags to survey data to test for patterns in positive and negative interactions among plants in a Michigan dry sand prairie. We hypothesized that interactions would be generally facilitative in this dry environment. Results indicate that most immediate (direct) interactions among dominant species are actually competitive, although interactions were more facilitative over the drier summer season. Interestingly, lagged density dependence was strong for all species in both seasons; it was positive for conspecific interactions, and both positive and negative for heterospecific interactions. Observed lagged density dependence is likely due to effects from litter and/or effects from past storage in rhizomes. Conspecific immediate and lagged interactions tended to be stronger than heterospecific interactions, suggesting that population dynamics in this community are driven mostly by conspecifics. Overall, the presence of strong lagged density dependence in this system suggests it may be more widespread in plants than previously thought.

Introduction

Both facilitative and competitive interactions have been demonstrated to occur among individual plants and are thought to influence community structure and dynamics. Facilitative and competitive mechanisms can operate simultaneously, and the net balance between them can change among environments, over time, and among different pairs of species (Bertness and Callaway 1994; Brooker and Callaghan 1998; Callaway and Walker 1997). Experimental research on competition and facilitation has typically assessed individual growth under controlled conditions over a single or few growing seasons (Brooker et al. 2008; Goldberg and Barton 1992; Gurevitch et al. 1992; Maestre et al. 2005). It is therefore not clear whether and how these interactions affect population and community dynamics in the field, and whether the balance of facilitation and competition at these levels is predictably patterned over time.

A different approach used by recent studies to measure species interactions at the population level is to fit dynamical models to field survey data (Adler et al. 2006; Freckleton and Watkinson 2001; Freckleton et al. 2000; Law et al. 1997; Rees et al. 1996). This approach uses the natural variation in species abundances in space and time to estimate conspecific and heterospecific interaction coefficients. Using this method, the species interactions in a variety of communities have been found to be predominantly negative (competitive), for example, in an annual pasture community (Freckleton et al. 2000), a perennial montane grassland (Law et al. 1997), and a mixed-grass prairie (Adler et al. 2006). Among sand dune annuals, species effects on the growth component of the population model are negative but effects on survival are positive (Rees et al. 1996).

The prevalence of competitive interactions in model-fitting studies contrasts with many manipulative experiments, which often find facilitative effects of neighbor plants on individual plant growth and, especially, survival. These facilitative interactions are sometimes more prevalent in, although not restricted to, stressful environments (Bertness and Callaway 1994; Goldberg et al. 1999; Maestre et al. 2005). This discrepancy between experimental and model-fitting studies suggests that more complex population dynamics models that separate different life history stages or time periods might well uncover positive interactions. For example, Rees et al. (1996) detected positive interactions in models that separated effects on growth and survival, and Adler and HilleRisLambers (2008) found more facilitative effects of neighbors on recruitment than survival when analyzed separately.

Similarly, when model-fitting studies allow interaction coefficients to differ among years, they often uncover some positive interactions and find that interactions can vary in direction and magnitude over time (Rees et al. 1996). This variability is often related to interannual variability in climate. Specifically, facilitative interactions are found in drier years (Adler et al. 2006) or competitive effects are reduced during extreme drought (Freckleton et al. 2000). This is consistent with Bertness and Callaway's (1994) abiotic stress hypothesis that facilitation dominates when environmental conditions are harsh while competition dominates when conditions are benign, however this idea has been much debated (Brooker et al. 2008). The abiotic stress hypothesis could also be extended to seasonal variability, that is, competition and facilitation may vary over the growing season due to seasonal fluctuations in environmental stress (Brooker and Callaghan 1998). Stress can fluctuate predictably and widely over the annual cycles, although this has not yet been investigated using model-fitting techniques.

The abiotic stress hypothesis is based on the idea that plants have multiple effects on the environment and the relative importance of different mechanisms depends on environmental conditions (Bertness and Callaway 1994). For example, plants can simultaneously reduce soil moisture, nutrients, and light through resource uptake but positively affect soil moisture and temperature by shading. In non-stressful, cool/wet environments, competition will dominate because plants are rapidly depleting nutrients and light, while the positive effects of shade are small because moisture and temperature are not limiting. However, under stressful, hot/dry conditions, shade's influence on moisture retention and temperature dominates over uptake; thus the net effect of a neighbor is facilitative.

As with interactions that occur directly among live plants, interactions that occur through plant litter can be a balance of positive and negative mechanisms operating simultaneously. Litter can facilitate plant growth through soil moisture retention (Holzapfel and Mahall 1999; Violle et al. 2006), temperature amelioration (Eckstein and Donath 2005), and nitrogen input to the soil (Belsky 1994; Garcia-Moya and McKell 1970). It can also inhibit plants due to light reduction and physical blocking (Facelli and Pickett 1991; Foster and Gross 1997). While litter is argued to be important in structuring plant communities (Facelli and Pickett 1991; Xiong and Nilsson 1999), again much experimental data is on an individual level.

One way to test for the effects of litter on community dynamics is to test for time-lagged density dependence in models, because the amount of litter at any given time should be correlated with live plant density in the past. This essentially breaks down the interaction coefficient into an immediate (or direct) interaction and a lagged interaction.

Although rarely tested in plants, Brook and Bradshaw (2006) included 30 plant species in a compilation of mostly animal population data sets in a study that tested lagged density dependence (1198 species in total). They found that 7-30% of the plant species exhibited lagged density dependence depending on the method of model selection. Other studies have found negative delayed density dependence in annual plants (Crone and Taylor 1996; Gonzalez-Andujar et al. 2006) or that including litter pools in models is necessary to predict plant population dynamics (Molofsky et al. 2000; Tilman and Wedin 1991). In fact, in one case the effect from litter overwhelmed the effect of immediate density dependence (Molofsky et al. 2000). In contrast to these relatively few examples in plants, delayed density dependence is commonly tested for and found in animal populations (Brook and Bradshaw 2006; Turchin 1990; Zeng et al. 1998). Interpretation of delayed density dependence may be different and more complex for plant populations, because it not only can reflect delayed competition (e.g., due to sequestration of resources) or interaction with natural enemies; it can also reflect the effects of the dead plant material itself or delayed positive effects from past storage of resources.

In this study, we investigate patterns in the balance of positive and negative interactions by fitting population growth models to community dynamics data derived from a small-scale permanent transect in a dry sand prairie in Michigan. Our goal is to understand processes underlying the dynamics in this system by breaking down the interaction coefficients to test how seasonality, yearly variation, and time lags influence the balance of competition and facilitation. Due to the hot, dry, harsh environment in this system and based on the abiotic stress hypothesis (Bertness and Callaway 1994), we hypothesize that 1) immediate interactions among species will be primarily facilitative, 2) interactions over the drier summer will be more positive than over the wetter fall/spring, and 3) lagged interactions will be facilitative because of effects from litter.

Methods

Study system and field survey

Our study system is a native grassland in the dry sand prairie of the northern lower peninsula of Michigan near the city of Indian River (latitude 45°23'26"N, longitude 84°35'41"W). The dry sand prairie ecosystem is interspersed with jack pine barrens in the sandy soils of the interior of Michigan's lower peninsula (Kost et al. 2007), and our study site is a patchy mosaic of grassland, shrub (*Arctostaphylos uva-ursi*, bearberry; *Prunus spp.*, cherry; *Amelanchier arborea*, serviceberry; *Comptonia peregrina*, sweet fern), jack pine (*Pinus banskiana*), and planted red pine (*Pinus resinosa*). It is located on a glacial outwash plain with excessively well-drained, droughty, sandy soil (Albert 1995) that is very nutrient poor with 3% soil organic matter (Farrer, *unpublished data*). The combination of low nutrients and organic matter, sandy soil, frequent droughts, and growing season frosts makes this ecosystem fairly stressful overall (Kost 2004). The site has not burned in over 50 years (Michigan Department of Natural Resources, *personal communication*). We include in the model the dominant species in the grassland, which make up over 90% of the stems: *Carex pensylvanica* (Pennsylvania sedge), *Danthonia spicata* (poverty grass), *Schizachyrium scoparium* (little bluestem), *Hieracium piloselloides* (yellow hawkweed), and *Cladina spp.* (reindeer lichen). The three dominant graminoids are native to grasslands and open canopy habitats throughout North America and are characteristic of dry sand prairie (Kashian et al. 2003; Kost et al. 2007).

Hieracium piloselloides is an exotic from Europe; it tends not to be invasive and in fact is the rarest of the four species in the grassland. *Carex*, *Danthonia* (C3 grass), and *Hieracium* all flower primarily in June, while *Schizachyrium* (C4 grass) flowers in September. *Cladina spp.*, reindeer lichens, are dominants in boreal systems, and are important components in this system occurring at about 30 percent cover. Less common species not included in the model are *Panicum depauperatum* (starved panic grass), *Oryzopsis pungens* (mountain ricegrass), *Campanula rotundifolia* (bluebell bellflower), and *Solidago spp*. (goldenrod). Nomenclature follows Voss (1972; 1984; 1997).

We censused a permanent transect (0.75 m by 4.5 m) for four years (2005-2008) two times per year (mid-June and mid-August) by overlaying a 3×3 cm grid over the transect and counting rooted stems in all cells (3750 total cells). Lichen was assessed in each cell on a scale of 0-4 based on the number of quadrats of the cell in which it was present. Although this is a fairly species-poor community overall, at the small scale it can be diverse with up to 3 plant species in a single 3×3 cm grid cell. Grid cell size was chosen to be 3×3 cm, because the plants in this system are generally small (height range 2 cm – 25 cm for vegetative growth) and many stems (up to 29) can be found in a 3×3 cm area. This small size also leaves the option of collapsing the data or using competition kernels if larger areas were desired. Law et al. (1997) successfully used a similar scale grid (3.3×3.3 cm) for their grassland survey designed to model competitive interactions. Despite the small total area of the transect (3.375 m^2), we carefully chose a location within the grassland that was representative of the community in the rest of the site. For example, species abundance distributions in the 3×3 cm grid cells were similar to another same-sized transect laid out in the site approximately 100 m away; however

Schizachyrium and *Hieracium* switched in rank abundance. Also, maximum densities in the 3×3 cm grid cells for each species were nearly identical (within one stem) to maximum densities in other small plots throughout an 80×80 m area that were selected specifically to contain dense patches of the species. Although no environmental measurements were taken in this transect, the mean and range of soil organic matter measurements in the other same-sized transect (mean 2.9%, range 1.8-5.0%, n=105) was similar to that throughout the 80×80 m study area (mean 2.9%, range 1.7-6.2%, n=120) suggesting that the range of soil conditions in a 3.375 m^2 area is representative of the grassland as a whole.

This system has a short growing season of about 100 days, from late-May to early-September (Eichenlaub et al. 1990). The spring (May to mid-June) has milder temperatures and more rain than the summer (mid-June to mid-August), which is hot and dry. The fall (mid-August to September) is also cool and wetter. All herbaceous perennials in this system tend to grow rapidly in the spring, but decline in aboveground density over the hot summer, and exhibit some regrowth in the fall (*personal observation*). All aboveground tissues of herbaceous plants senesce over the winter. We will refer to June to August growth as "summer" and the growth from August to the following June as "fall/spring"; the fall/spring growth mainly includes growth that occurs in the spring but also includes any regrowth (or storage from the regrowth) at the very end of the growing season following the August census.

Model structure

We formulated a family of models of the growth and spread of each of the four plant species within each season, fit various models in this family to the data by maximum likelihood, and evaluated the relative weight of the evidence in favor of each model using the Akaike Information Criterion (AIC). We fully describe the family of models here. In the following, subscripts i, j range over species, subscripts x, y over grid cells, and t over time. Odd times ($t = 1, 3, 5, 7$) refer to spring censuses; even times ($t = 2, 4, 6, 8$) to fall censuses. Let $N_{i,x,t}$ denote the density of species i in cell x at time t. All our models assume that

$$N_{i,x,t} \sim \mathrm{negbin}(\mu_{i,x,t}, k_{i,x,t}), \tag{1}$$

i.e., that $N_{i,x,t}$ is a negative binomial random variable with mean $\mu_{i,x,t}$ and size parameter $k_{i,x,t}$ (and therefore with variance $\mu_{i,x,t} (1 + \mu_{i,x,t} / k_{i,x,t})$). Each model predicts next season's population densities in terms of three factors: (i) density-dependent growth within each cell, (ii) short-distance colonization by clonal ingrowth from neighboring cells, (iii) long-distance colonization by seed (Eq. 2). Because we did not distinguish among these types of recruitment in the field survey, parameters describing each of these components in the model are estimated simultaneously by maximum likelihood. Specifically, in each model, the expected value of $N_{i,x,t}$ is of the form

$$\mu_{i,x,t} = \underbrace{(1 - d_{i,t-1}) G_{i,x,t-1}}_{\text{(i)}} + \underbrace{\frac{d_{i,t-1}}{8} \sum_y G_{i,y,t-1}}_{\text{(ii)}} + \underbrace{c_{i,t-1}}_{\text{(iii)}}, \tag{2}$$

where $d_{i,t-1}$ is the fraction of shoots that emigrate from each cell over the season $t-1$ to t, $G_{i,y,t-1}$ models clonal growth, the sum is taken over the neighboring 8 cells, and $c_{i,t-1}$ is colonization by seed over the same time period. We use a variant of the Ricker model for density dependent clonal growth:

$$G_{i,x,t} = N_{i,x,t} \exp\left(r_{i,t} + \sum_j \sum_\ell \alpha_{ij,\ell,t} N_{j,x,t-\ell} \right). \quad (3)$$

Here, $r_{i,t}$ is the intrinsic growth rate of species i at time t. The sums are taken over species j and time-lags ℓ, respectively, and $\alpha_{ij,\ell,t}$ represents the per capita effect of species j on the growth of species i at lag ℓ and time t. We refer to α's as "interaction coefficients", similar to "competition coefficients" except positive values of α correspond to facilitation, negative values to competition. We examined models including immediate density dependence ($\ell = 0$), and lags of up to one full year ($\ell \leq 2$). Although we did not model lichen growth because it is very slow (a few mm per year), we did include the effects of lichen on the four focal species.

We used the negative binomial distribution (Eq. 1) because it allows for us to model the variance independently of the mean (White and Bennetts 1996); our data were overdispersed compared to a Poisson distribution (in which the variance equals the mean). Specifically, we assumed that the size parameter k was linearly related to density:

$$k_{i,x,t} = k^0{}_{i,t} + k^1{}_{i,t} N_{i,x,t}. \quad (4)$$

This allowed variance to decrease as density increased, because exploratory data analysis showed grid cell populations with low densities tended to be much more variable than those with high densities. Note that the coefficients of this relationship are independent of cell location x.

Within this family of models, seasonal and interannual variability can be accounted for by allowing the parameters $r_{i,t}$, $d_{i,t}$, $c_{i,t}$, $\alpha_{ij,\ell,t}$, $k^0{}_{i,t}$, $k^1{}_{i,t}$ to vary with t. We also explicitly consider models with seasonality only (and no interannual variability) by requiring $r_{i,t} = r_{i,t-2}$ for all t, and similarly for the other parameters.

In the models investigated in this paper, species interact directly only with other individuals sharing the same 3×3 cm grid cell. For each target species, we explored models with a spatial interaction kernel (an exponential kernel with a cutoff) so that plants interacted with individuals outside of their grid cell, both with and without time lags. Surprisingly, in only one case did the spatial model perform substantially better (ΔAIC > 4) than non-spatial models, therefore only models with non-spatial competition are presented here.

In these models, we assume that demographic parameters (r, d, c) and interaction coefficients (α*'s*) are constant throughout space (within a given time period). Although unmeasured spatial heterogeneity in soil or microtopography may affect parameter values and contribute to estimation error, there is no reason to expect that this spatial heterogeneity would result in consistent differences between immediate and lagged coefficients or between seasons and years.

Model analysis

The statistical software R (R Development Core Team 2008) package bbmle (Bolker 2008b) was used to fit the models using maximum likelihood. The grid cells on the perimeter of the transect were not included as target cells, but were included as neighboring cells and so allowed to influence clonal ingrowth. All interior grid cells were used for parameter estimation.

To test whether time lags should be included in models and whether parameters should vary among years, AIC was used to compare models. AIC tests whether more parameters (time lags or yearly coefficients) should be included in a model by penalizing based on the number of parameters added, so as not to overparameterize models. AIC was chosen because most models were not nested, so likelihood ratio tests could not be used. Also, the sample size in this data set is very large (3404 grid cells for each census, not including perimeter cells). When sample size is large, the Bayesian Information Criterion (BIC) is over-conservative and tends to choose the model with fewest parameters as the best model (Lindsey 1999). It is generally accepted that models within 2 AIC of each other are equivalent (Bolker 2008a), so we do not make a distinction among models this close in AIC.

Four different types of time lags were explored for each season: 1) a lag from the previous season only, 2) a lag from the previous year only, 3) a model with both seasonal and annual lags and different interaction coefficients for both, and 4) a model with both lags but with the same interaction coefficients for both. We compared these four lagged models with a model that did not include any lagged coefficients using AIC (models (a) through (e) in Table 3A1.1, see Appendix 1 for a list of parameter restrictions for each of the models). For both fall/spring and summer and for all species, the model with the lag from the previous season only was either the best model by AIC or within 2 AIC (Table 3A2.1). This means that, for example, for the summer transition from June 2006 to August 2006, the best model included the lag from August 2005. Thus for all subsequent model fitting and investigation, a lag of one season was used.

Yearly variability was explored by allowing parameters to differ in values for each year; this asks whether all summers (or all fall/springs) have the same dynamics. Three different types of yearly variability were assessed: 1) variable demographic parameters (c, r, d) and constant interaction coefficients (α's), 2) constant demographic parameters and variable interaction coefficients, and 3) variable demographic parameters and variable interaction coefficients. These three models were compared to a model with constant interaction coefficients and constant demographic parameters using AIC (models (b), (f), (g), and (h) in Table 3A1.1).

The estimated values for some interaction coefficients were near zero and/or had large standard errors associated with them (standard error was estimated using the quadratic approximation to the likelihood in package bbmle); thus these species interactions likely do not play an important role in community dynamics. To determine which interaction coefficients were important, we started with a model that included all interaction coefficients and systematically deleted interaction coefficients with the largest standard errors one at a time, refitting the model after each deletion. When standard errors for two coefficients were similar, we tried both orders of deleting coefficients. Because parameters were typically not highly correlated, the order of deletion did not affect the outcome of model selection. AIC was used to compare all of these models, and we report models within 4 AIC of the best model, so that we are not too conservative in judging a parameter to be zero.

We ensured that we found global maxima to our parameter estimates by using a multistart, multistep optimization strategy (for details see "Global maxima optimization strategy" in Appendix 3). Also, although parameter correlations exist, profiling analyses indicated that they did not qualitatively affect results (see "Univariate profiling" in Appendix 3).

Model performance

We assessed the ability of our models to produce realistic dynamics by simulating the "best" models in a coupled map lattice. The size of the area in the simulation was the same as the field transect (150 × 25 grid cells). We initiated the simulation with densities from time steps 1 and 2, and simulated for 6 more time steps (3 years). One thousand simulations were done. The mean and 95% confidence intervals were obtained for total population trajectories and histograms of grid cell population densities in the eighth time step and were compared to actual values. We did not extrapolate to longer time periods, because we do not believe we have sufficient information on interannual variability to credibly extrapolate.

Results

The four species display seasonal fluctuations in total population size in the transect over the four-year period (Fig. 3.1, black lines). They differ, however, in their responses to interannual variability, especially in the final year of the census when *Danthonia* increases dramatically.

Time lags

In models without time lags, a few of the interaction coefficients are positive, especially in the summer (Table 3.1, Table 3A4.1 for standard errors). However, for all species, adding one-season time lags to both summer and fall/spring models increased the fit of the models by 2-85 AIC units despite adding five extra parameters (Table 3A2.1), thus all subsequent analyses include one-season lags. Adding time lags to the models shifted some positive and negative interactions to lagged coefficients and uncovered new positive interactions that were lagged. This resulted in the interesting trend that immediate interaction coefficients tend to be negative, while lagged interactions tend to be positive (Table 3.2, Table 3A4.2 for standard errors). For example, only three summer (15%) and two fall/spring (10%) immediate coefficients are positive, while for lagged interactions, nine summer (45%) and six fall/spring (30%) are positive (Table 3.2). This trend was driven mainly by the conspecific lagged interactions, which were all positive.

Conspecific vs. heterospecific interactions

Conspecific immediate interaction coefficients were always included in the best models by AIC, and they were always negative (Table 3.2). Heterospecific immediate interactions were only sometimes included in the best models (7/16 in summer and 7/16 in fall/spring) and were about half negative/half positive. Thus, overall, conspecific interactions tend to be more negative than heterospecific interactions.

As with immediate interactions, lagged conspecific coefficients were always included in the best model for all species, while lagged heterospecific coefficients were only sometimes included (9/16 in summer, 7/16 in winter) (Table 3.2). Lagged conspecific interactions tended to be more positive than lagged heterospecific interactions.

We examined two sources of potential bias which may have resulted in the greater inclusion of conspecific relative to heterospecific interaction coefficients in the best models: sample size and range of neighbor densities. Conspecific interactions have larger sample sizes (number of occurrences) than heterospecific interactions due to intraspecific aggregation, so they may be better estimated and more likely to be included in best models. To visualize whether sample size affected the inclusion of coefficients, we plotted the sample sizes of non-included vs. included interaction coefficients (formal statistical tests are not appropriate) (Fig. 3.2a). Indeed, pairwise interactions with large sample sizes tended to be more often included in the best model. However, not all coefficients with large sample sizes were included (range 10-3935) and not all coefficients with small sample sizes were excluded (range 11-1975).

Similarly, interaction coefficients based on a broader range of neighbor densities may be better estimated and more likely to be included in best models. Plotting the maximum neighbor densities for non-included vs. included interaction coefficients showed that most species experienced a wide range of neighbor densities, and this did not tend to influence inclusion of the coefficient by AIC (range of included densities 1-29, range of non-included densities 2-27, Fig. 3.2b).

Seasonality

The two seasons display very different dynamics. From June to August, all species decline in population size (population growth rate r is negative), while in fall/spring all populations increase (Table 3.3, Table 3A4.3 for standard errors). Also, both short- (d) and long-distance (c) colonization rates tend to be lower in summer than in fall/spring. Facilitation tends to be more prevalent and competition less intense in the summer compared to the fall/spring (Table 3.2). For example, 12 of the 40 interaction coefficients are positive in the summer vs. 8 in the fall/spring, and the negative interaction coefficients in summer are less negative than those in fall/spring.

Yearly variability

Adding different demographic parameters (population growth rate *r*, short-distance colonization *d*, long-distance colonization *c*) for each of the three summers increased the fit of the models for all species, despite adding six extra parameters (Table 3A2.2). In contrast, adding different interaction coefficients for each of the three summers did not increase model fit by AIC (20 extra parameters), indicating that competitive and facilitative interactions were similar across all three summers (Table 3A2.2).

Dynamics in the fall/spring were less consistent among years for the four species. For *Carex*, the best fall/spring model included both constant demographic parameters and constant interaction coefficients; for *Danthonia*, and *Hieracium* the best model included variable demographic parameters and constant interaction coefficients; and for *Schizachyrium*, the best model included constant demographic parameters and variable interaction coefficients (Table 3A2.2). For *Schizachyrium*, the main differences among years were the changes in effect of *Danthonia*, *Hieracium*, and lichen from positive or neutral in fall/spring 1 and 2 to negative in fall/spring 3 (data not shown).

Model performance

Coupled map lattice simulations of the best models produce realistic dynamics. The models accurately capture total population fluctuations and trends over the 8 time periods for all species (Fig. 3.1). The models are also fairly good at producing grid cell population density distributions similar to the actual distributions in the eighth time step

(Fig. 3.3); however some differences are apparent. The model tends to overestimate the number of zeros and underestimate the number of cells with one and two stems for *Carex* and *Hieracium*, and overestimates the number of cells with one and two stems for *Danthonia*.

Discussion

As in many experimental studies but contrary to model-fitting studies to date, we find positive interactions among species in this environmentally stressful system. We uncovered these positive interactions by allowing for seasonality and time lags in our models. In fact, contrary to our hypothesis, few immediate interactions in this community are positive, although more interactions are positive and competition is relatively weak over the drier, hotter, summer season. In contrast, time-lagged interactions are strong and primarily positive. These results are compatible with the Bertness and Callaway's (1994) abiotic stress hypothesis, but this analysis separates immediate and lagged interactions. Below we discuss the effects of time lags, seasonality, and interannual variation on species interactions and community dynamics, possible mechanisms that could produce these dynamics, and implications for this community and more broadly.

Time lags

Time lags are important in the dynamics of all species in this community in both summer and fall/spring. The most striking pattern is that all conspecific and many heterospecific lagged effects are positive. For conspecific lagged interactions, two different processes may produce this strong positive effect: past storage in rhizomes and facilitative effects of litter. The four plant species all store nutrients and carbohydrates in rhizomes. Thus, the size of the past populations (lagged densities) of a species is indicative of the amount of energy they would have stored in their rhizomes from previous growth. Although we did not model energy transfer explicitly, this effect could contribute to the lagged coefficient. So, while conspecific ramets compete strongly within a season (negative immediate interactions), any past population densities may have a positive effect on current growth.

Conspecific lagged interactions may also be caused by litter; this mechanism is also the most likely for heterospecific lagged interactions. Populations tend to decline over the summer, producing some amount of litter, and at the end of the growing season in fall, all aboveground biomass senesces, producing litter. The lagged population density is therefore related to the amount of litter currently present in the grid cell.

Aboveground litter may facilitate plant growth because it ameliorates high temperatures and retains soil moisture (e.g., Facelli and Pickett 1991; Fowler 1986; Holzapfel and Mahall 1999). Above- and below-ground litter could also facilitate growth due to nutrient release from decomposition. Consistent with these mechanisms, other correlative data from this system suggest that microsites with high aboveground litter are associated with lower soil temperature, higher soil moisture in the summer (non-significant trend), and higher available soil nitrogen (E.C. Farrer, *unpublished data*). Nevertheless, several of the lagged effects from heterospecifics were negative (four in summer and five in fall/spring). Negative lagged interactions could be due to delayed competition, because individuals have sequestered nutrients, which are no longer available for current plant growth. Probably more likely, the negative lagged effects could come from light reduction, because in this system aboveground litter is strongly negatively correlated with light (E.C. Farrer, *unpublished data*).

Lagged density dependence is rarely studied in plant populations, perhaps because some have argued it is unlikely due to the modularity and the lack of size thresholds in plant reproduction (Crawley 1990; Rees and Crawley 1989). When time lags have been incorporated in population dynamic models, studies suggest that lagged interactions are not very common, and when they do occur, both positive and negative lagged effects have been found. For example, in a study of 30 plant populations (all perennials), delayed density dependence was found in only 7-30% of the populations (Brook and Bradshaw 2006). The lagged density dependence was positive in a little over half of these cases (Brook and Bradshaw 2006, B.W. Brook, *personal communication*). However, negative lagged density dependence was found in two modeling-fitting studies of annual weeds (Crone and Taylor 1996; Gonzalez-Andujar et al. 2006). Two other studies that included a litter pool explicitly in population dynamics models found negative effects of litter on plant population biomass (Molofsky et al. 2000; Tilman and Wedin 1991).

In contrast to these studies, we found conspecific lagged effects to be strong and positive for all four species, and heterospecific lagged effects occurred and were both positive and negative. Our study has two main differences that may have increased our ability to pick up this signal of delayed density dependence. First, our census and our model are very local in space, at the cm scale over which individual plants interact. Surveys at larger scales may not detect lagged density dependence (or even immediate density dependence) because those interactions do not occur at those scales. Second, most populations in model-fitting studies are censused yearly, whereas our study populations were censused twice a year. Delayed interactions through litter or rhizome storage may decay over time, so the interactions may be too weak to detect with yearly censuses. In support of this, we found best model fits with a seasonal, not annual, lag.

The presence of positive lagged interactions in our study may be due to the stressful abiotic environment in the dry sand prairie, in which the net effect of litter would tend toward facilitative. Consistent with this, the negative litter effects of Tilman and Wedin (1991) were only found at high productivity, when the net effect of litter is negative due to decreased light. Positive conspecific lags in our study are likely also influenced by the perennial nature of the plants and the consequent rhizome storage effect. Most of the previous studies that detected negative lagged density dependence studied annual plants (Crone and Taylor 1996; Gonzalez-Andujar et al. 2006; Molofsky et al. 2000).

Theoretical studies that investigate the implications of lagged interactions for population dynamics typically investigate negative delayed density dependence. These studies have demonstrated that lags in negative density dependence can produce a range of complex dynamics including damped oscillations, periodic dynamics, and chaos (Kot 2001; May et al. 1974), and in general tend to decrease stability of the system (Crone 1997). This whole range of dynamics has been observed in models parameterized from animal populations (Lima et al. 1999; Turchin and Taylor 1992) as well as plant populations (Crone and Taylor 1996; Molofsky et al. 2000; Tilman and Wedin 1991). No studies to our knowledge have analyzed the dynamic consequences of positive delayed density dependence; Pastor and Walker (2006) showed that time lags due to the delay in nutrient release from litter can lead to damped or bounded oscillations in plants. Preliminary simulations of simplified single-species versions of the models presented here suggest that the consequences of positive lagged interactions depends on their magnitude relative to negative immediate interactions; for example, when the magnitude of the positive lagged coefficient is larger or similar to that of negative immediate coefficient, population cycles and explosions occur. This suggests that interactions at very local scales can influence the dynamics of the population as a whole, although future rigorous simulations of these models will address these questions more comprehensively.

In this study, incorporating lagged interactions in models suggested new processes important for population dynamics, such as litter effects and rhizome storage. Interestingly, simulations of the best models without time lags also produced fairly reasonable dynamics over the 8 time steps, however these models obscure the mechanisms through which interactions occur. This study informs future theoretical and experimental studies that lagged interactions may commonly occur in nature, can be quantified, and their implications can be tested.

Conspecific vs. heterospecific interactions

Conspecific interactions tended to be large in magnitude and were included in the best model by AIC in both seasons for all four species. Heterospecific interactions, however, were less commonly included (16/32 included in summer, 14/32 included in fall/spring), suggesting that population dynamics are mainly driven by conspecifics. This was affected to some extent by sample sizes of the pairwise interactions, although most sample sizes were large (mean sample size 478, range 10 to 3935), and most of the non-included interaction coefficients were small in magnitude indicating that they were weak. Nevertheless, all species were affected by at least two heterospecifics in both summer and fall/spring, suggesting that interactions with heterospecifics through live plants or their litter play a modest role in the dynamics of this community. One exception to the above pattern is that *Hieracium* tends to have large magnitude effects, both positive and negative, on other species. *Hieracium's* biomass per individual is 2-3 times that of the other species, which may cause these large per capita effects.

In nearly all cases, conspecific immediate interactions were more negative than heterospecific interactions. This pattern is expected for coexisting species under classical models of niche partitioning and has also been found in a similarly dry, nutrient poor sand dune community (Rees et al. 1996), among functional groups in an Australian pasture community (Freckleton et al. 2000), and in mixed grass prairie (Adler and HilleRisLambers 2008), but not in a montane grassland (Law et al. 1997). The four species differ in their growth form (runner vs. clumper), photosynthetic pathway (C_3 vs. C_4), tissue chemistry (e.g., C:N ratio, E.C. Farrer, *unpublished data*), and may occupy different temporal niches (flowering in June vs. August). The negative conspecific interactions may also be attributed to negative plant-soil feedback due to species-specific soil pathogens (Bever et al. 1997), although if this were occurring and important, lagged conspecific interactions would not be expected to be positive.

The implications of stronger conspecific than heterospecific immediate interactions for stable coexistence, however, are unclear because the lagged coefficients show quite a different pattern: conspecific lagged coefficients tend to be more positive than heterospecific lagged coefficients. This may be because conspecific lagged interactions are the combined effects of rhizome storage (positive) and litter (positive or negative), while heterospecific lags can only be from litter. While other studies have found that positive immediate conspecific (Molofsky et al. 2001) and heterospecific (Gross 2008) interactions can promote coexistence or delay competitive exclusion, it is unclear how models with lagged positive interactions will behave.

Seasonality

Population dynamics in this dry grassland community were cyclic over the year and correspond to differences in precipitation and temperature between the two seasons (Table 3.4). Populations of all species decline over the hot summer and regrow over the rainier, cooler fall and spring. Seedling establishment (long-distance colonization) and clonal expansion (short-distance colonization) were also more common over the fall/spring. Competition varied between the two seasons, with more facilitation and weaker competition in the summer. Kikvidze et al. (2006) and Sthultz et al. (2007) found similar seasonal variation in interaction intensity and direction in experiments.

Measuring interactions and growth dynamics over different seasons may uncover interactions and dynamics that would otherwise be weak or cancel out if they were averaged over a year (e.g., if communities were censused on a yearly basis). Understanding that yearly dynamics are the net effect of two quite different seasonal dynamics for each species may help to explain some of their year-to-year variation. Seasonality may also have implications for the coexistence of species in this system, not only because species may adapt to different seasonal niches, but also because the summer drought particular to this system is a type of disturbance. This disturbance may act to reset interactions among species, maintaining the system in a non-equilibrium state, which may slow competitive exclusion (Kikvidze et al. 2006).

Interannual variability

Even within a season, demographic parameters (growth rate, short- and long-distance colonization) often varied among the three different years. This is likely due to annual variation in climatic variables such as temperature and precipitation. For example, *Danthonia* and *Hieracium* had higher growth rates and germination rates in fall/spring 3 compared to fall/spring 1 and 2; this corresponded to a spring that was cooler by 2 degrees and very wet compared to the previous two springs (Table 3.4). Other model-fitting studies have also found that demographic parameters often vary among years (Freckleton et al. 2000; Rees et al. 1996) and that species correlate with different seasonal patterns of precipitation and temperature (Adler and HilleRisLambers 2008; Adler et al. 2006; Dunnett et al. 1998).

When testing variability in demographic parameters, we tested whether all parameters (r, d, and c) vary from year-to-year vs. none of the parameters vary. Nevertheless, the parameters may differ in their degree of interannual variability: parameter estimates show that growth rate and short-distance colonization vary interannually by a factor of 2 or 3, but that long-distance colonization by seed could vary by a factor of 20 or 40. This is reasonable because the dry conditions in the sand prairie often severely limit germination and establishment, but occasionally a rainy year causes a flush of seedlings.

Unlike demographic parameters, interaction coefficients did not vary among years, with only one exception (*Schizachyrium* in the fall/spring). This indicates that the intensity and direction of interaction (competition vs. facilitation) is fairly constant in this system regardless of environmental conditions. There is no clear pattern in the literature from other model-fitting or experimental studies as to whether interaction coefficients vary over time. Some studies find the net balance of competition and facilitation varies among years (Greenlee and Callaway 1996; Pugnaire and Lázaro 2000; Tielbörger and Kadmon 2000; Turnbull et al. 2004) and is related to environmental conditions (Adler et al. 2006), while other studies show constant (Casper 1996) or a mix of constant and variable interactions depending on the species (Rees et al. 1996).

The results from this study suggest that demographic parameters might be more susceptible than competition/facilitation to changes in environmental conditions. For example, a slight change in environment may not tip the balance in the net interaction among plants, if plants are competing for moisture and moisture remains limiting; however, the same change in environment may be enough to depress growth rates or germination rates. However, this result should be viewed with some caution for two reasons. First, demographic parameters may be better estimated than pairwise interaction coefficients due to larger sample sizes. Second, since there are fewer demographic parameters (3) than interaction coefficients (10), a model with yearly demographic parameters adds fewer parameters and thus is penalized less by AIC than a model with yearly interaction coefficients; so a model with variable interaction coefficients must increase the likelihood more to be chosen as the best model.

Conclusions

This study demonstrated that applying complex model-fitting techniques to field data can uncover complicated ecological interactions that would not be revealed by more simple tests. Specifically, we added different seasonal and lagged components to models of plant species interactions and uncovered new interactions, some of which were facilitative. We found patterns of lagged vs. immediate interactions that suggest new mechanisms that are important in driving community dynamics. Because plant litter plays an important role in many other plant communities and because many plant communities are dominated by perennials that store resources in rhizomes or roots, lagged density dependence many be a more wide-spread phenomenon in plants than previously thought.

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Table 3.1. Summer and fall/spring interaction coefficients (per capita effect of species in columns on species listed in rows) for the models without time lags. Abbreviations are as follows: *Carex* (C), *Danthonia* (D), *Schizachyrium* (S), *Hieracium* (H), and lichen (L). Interaction coefficients in bold indicate conspecific interactions; blank cells indicate that the interaction coefficient was not included in the best model (i.e. it is zero). The summer transitions are from three years, summers 2, 3, and 4. The fall/spring transitions are also from three years, fall/spring 1, 2, and 3. These transitions are from the same years as in the lagged models (Table 3.2) to allow comparison. All summer models have variable demographic parameters. In fall/spring models, *Carex* and *Schizachyrium* have constant demographic parameters, and *Danthonia* and *Hieracium* have variable demographic parameters.

		Interaction coefficient				
		C	D	S	H	L
Summer	C	**0.012**	-0.006			-0.007
	D	0.028		0.032	0.027	0.009
	S	0.010	-0.006	**-0.020**		-0.070
	H	0.053	-0.016		**-0.135**	-0.261
Fall/spring	C	**-0.029**	-0.019	-0.020	-0.005	-0.010
	D		**-0.013**	0.016	0.103	-0.023
	S	-0.071	-0.007	**-0.073**	-0.267	-0.021
	H	-0.114	-0.023	-0.094	**-0.156**	-0.118

Table 3.2. Summer and fall/spring interaction coefficients (per capita effect of species in columns on species listed in rows) for models with one season time lags. Interaction coefficients in bold indicate conspecific interactions; blank cells indicate that the interaction coefficient was not included in the best model (i.e. it is zero). All summer models have variable demographic parameters. In fall/spring models, *Carex* and *Schizachyrium* have constant demographic parameters, and *Danthonia* and *Hieracium* have variable demographic parameters.

		Interaction coefficient									
		C	D	S	H	L	C lag	D lag	S lag	H lag	L lag
Summer	C	**-0.071**		-0.035			**0.117**	-0.007	0.043	-0.045	
	D	0.025	**-0.030**	0.047			0.008	**0.044**	-0.028	0.115	0.030
	S			**-0.040**	0.121	-0.056			**0.035**	-0.306	
	H		-0.037		**-0.185**	-0.215		0.047		**0.302**	
Fall/ spring	C	**-0.178**				0.009	**0.166**	-0.017	-0.011		-0.021
	D		**-0.033**	0.032				**0.024**	-0.012	0.094	
	S	-0.060	-0.006	**-0.124**					**0.044**	-0.164	
	H	-0.089		-0.085	**-0.272**	-0.118				**0.128**	0.143

Table 3.3. Demographic parameters for the different species in summer and fall/spring. For each species, parameters are from the best model by AIC, so some have variable and some have constant demographic parameters. When three parameters are present, they correspond to summer 2, 3, and 4, and fall/spring 1, 2, and 3.

	Growth rate, *r*		Short-distance colonization rate, *d*		Long-distance colonization rate, *c*	
	Summer	Fall/spring	Summer	Fall/spring	Summer	Fall/spring
Carex	-0.2580	0.0587	0.1817	0.1698	0.0351	0.1084
	-0.1203		0.1346		0.0084	
	-0.1178		0.1196		0.0056	
Danthonia	-0.2167	0.1760	0.1409	0.1835	0.0030	0.0005
	-0.1102	0.3125	0.0738	0.1608	0.0011	0.0110
	-0.1105	0.4176	0.0388	0.1538	0.0015	0.0224
Schizachyrium	-0.0989	0.5015	0.2924	0.2073	0.0007	0.0004
	-0.3049		0.1650		0.0000	
	-0.2798		0.0968		0.0004	
Hieracium	-0.3124	0.6746	0.1901	0.1410	0.0000	0.0013
	-0.6448	0.6701	0.1108	0.1367	0.0000	0.0003
	-0.1977	1.2094	0.0801	0.2999	0.0000	0.0056

Table 3.4. Annual and seasonal variability in temperature and precipitation during the growing seasons of the four years of the survey; numbers are averages over each of the three seasons and can be directly related to model transitions over the summer and fall/spring.

	Summer mid-Jun – mid-Aug	Fall mid-Aug – Sep	Spring May – mid-Jun
Precipitation (cm/mo)			
Year 1, 05-06	5.4	11.8	7.7
Year 2, 06-07	6.9	9.8	5.4
Year 3, 07-08	5.5	9.0	10.3
Year 4, 08-09	5.8	6.3	
Temperature (mean daily max)			
Year 1, 05-06	27.6	22.2	21.0
Year 2, 06-07	27.1	20.2	22.6
Year 3, 07-08	26.3	22.4	18.8
Year 4, 08-09	24.7	22.1	

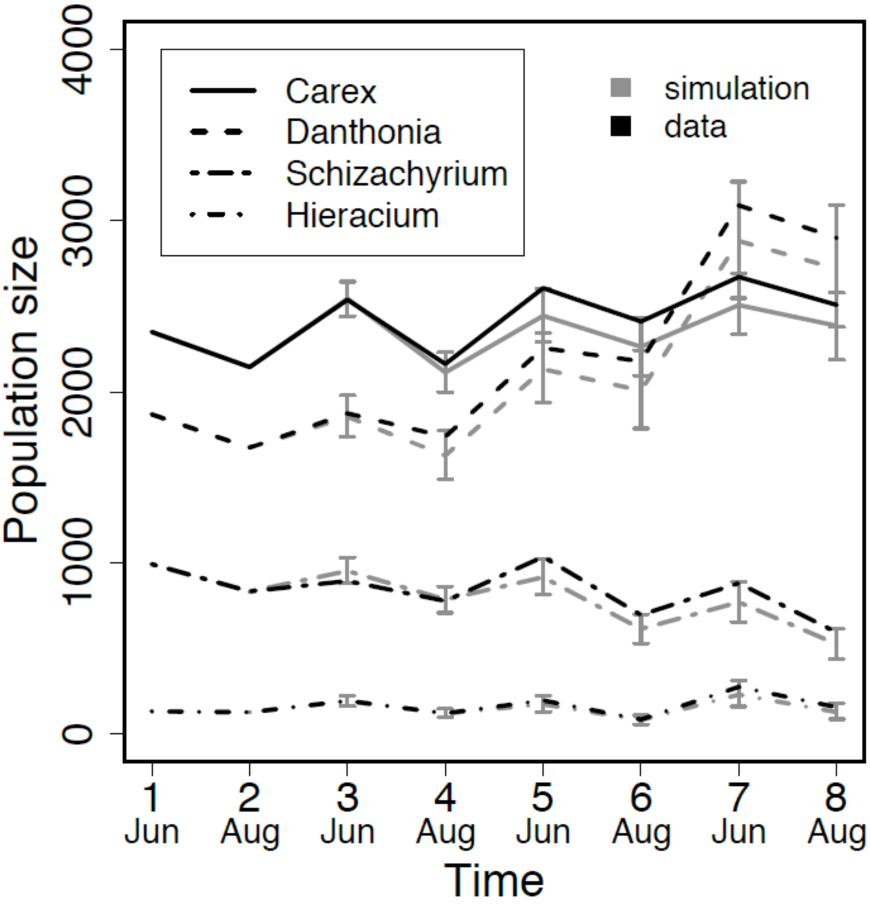


Fig. 3.1. Temporal dynamics in the four species' populations over the four-year census (June 2005-August 2008) (black lines) and results from simulations of the best models (gray lines). Odd times represent June censuses and even times represent August censuses. Populations are stem counts summed over the entire 0.75 × 4.5 m transect. Error bars represent 95% confidence intervals based on 1000 simulations.

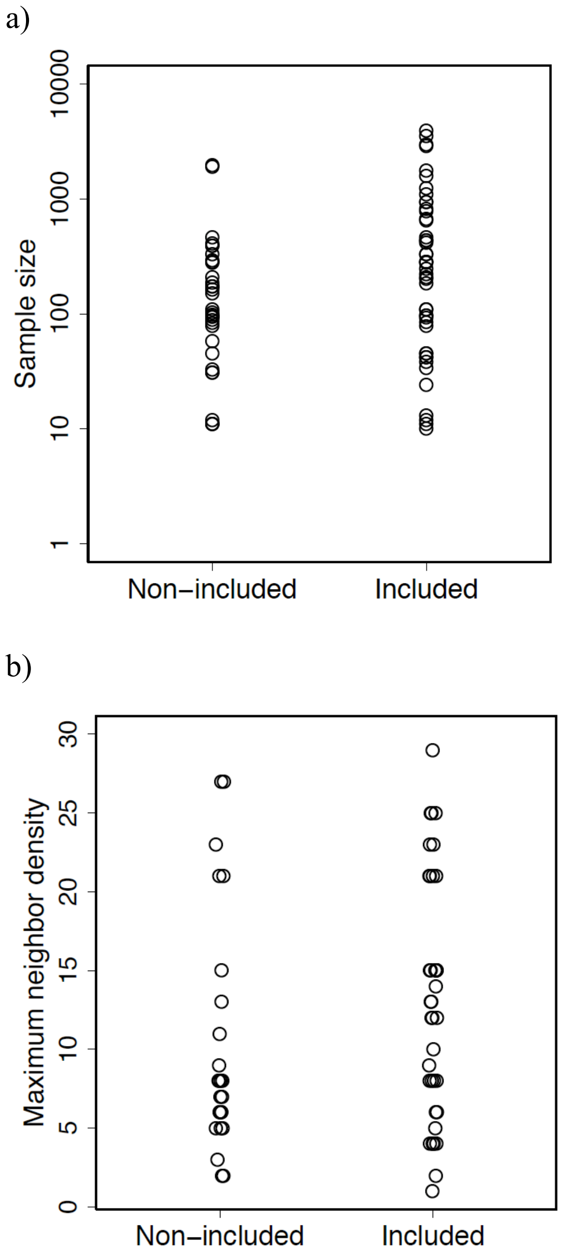
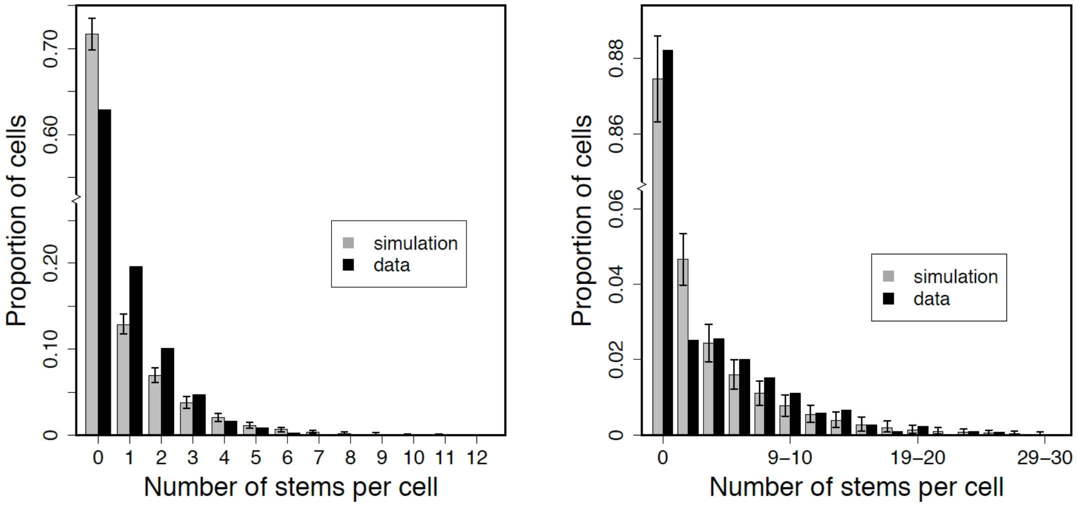


Fig. 3.2. Distribution of a) sample sizes and b) maximum neighbor densities of pairwise species interactions (pairwise co-occurrences in grid cells in the transect) that were not included or included in the best model by AIC. Sample sizes are on a log scale. Maximum neighbor densities do not include lichen as the neighbor, for which all species in both seasons were present with the maximum amount of lichen (4 quadrats) except for one (3 quadrats). Note that interaction coefficients that were included in models tended to have higher sample sizes, but there is considerable spread in both types of coefficients; and maximum neighbor density did not tend to influence inclusion of the coefficient.

a) *Carex* b) *Danthonia*



c) *Schizachyrium* d) *Hieracium*

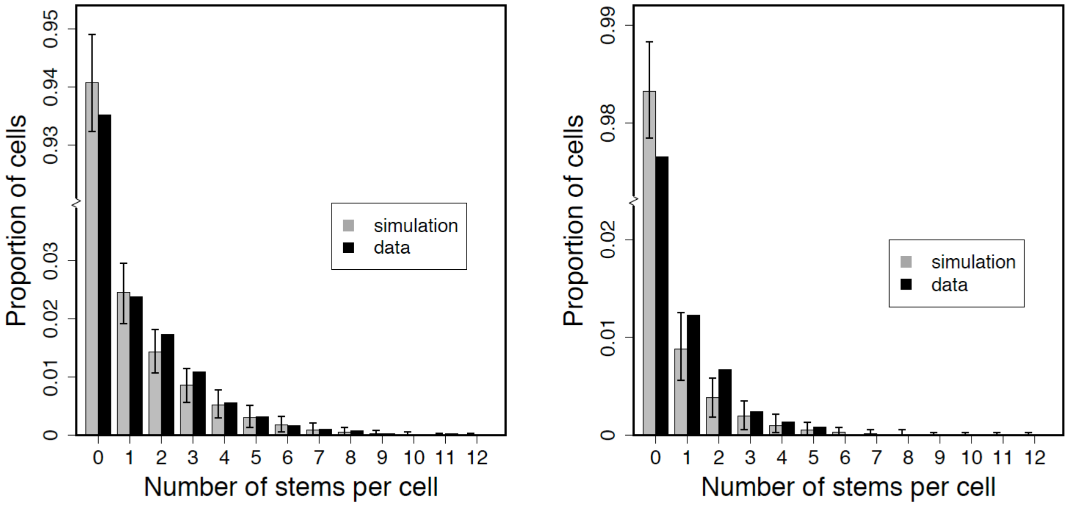


Fig. 3.3. Histograms of the distribution of grid cell stem densities in the last time step (August 2008) in the actual data and from simulations of the best models for a) *Carex*, b) *Danthonia*, c) *Schizachyrium*, and d) *Hieracium*. Error bars are 95% confidence intervals based on 1000 simulations.

Appendix 1. Parameter restrictions

Table 3A1.1. Description of parameter restrictions for the different models compared using AIC. Each of these tests was done separately for summer and fall/spring transitions; "dem" refers to demographic parameters. The variance parameters, $k^{0}_{i,t}$ and $k^{1}_{i,t}$, are always restricted by $k^{0}_{i,t} = k^{0}_{i,t-2}$ and $k^{1}_{i,t} = k^{1}_{i,t-2}$, so they are not listed here. Note that t-2 indicates one year ago (i.e., the same season).

Model	Parameter restrictions
a) No lag, no yearly variation in dem. parameters or α	$\alpha_{ij,\ell,t} = 0, \ell > 0$ and $\alpha_{ij,\ell,t} = \alpha_{ij,\ell,t-2}$ $c_{i,t} = c_{i,t-2}$ $d_{i,t} = d_{i,t-2}$ $r_{i,t} = r_{i,t-2}$
b) One season lag, no yearly variation in dem. parameters or α	$\alpha_{ij,\ell,t} = 0, \ell > 0$ and $\alpha_{ij,\ell,t} = \alpha_{ij,\ell,t-2}$ $c_{i,t} = c_{i,t-2}$ $d_{i,t} = d_{i,t-2}$ $r_{i,t} = r_{i,t-2}$
c) One year lag, no yearly variation in dem. parameters or α	$\alpha_{ij,\ell,t} = 0, \ell = 1$ and $\ell > 2$ and $\alpha_{ij,\ell,t} = \alpha_{ij,\ell,t-2}$ $c_{i,t} = c_{i,t-2}$ $d_{i,t} = d_{i,t-2}$ $r_{i,t} = r_{i,t-2}$
d) One season and one year lag with different parameters for both, no yearly variation in dem. parameters or α	$\alpha_{ij,\ell,t} = 0, \ell > 2$ $c_{i,t} = c_{i,t-2}$ $d_{i,t} = d_{i,t-2}$ $r_{i,t} = r_{i,t-2}$
e) One season and one year lag with same parameters for both, no yearly variation in dem. parameters or α	$\alpha_{ij,\ell,t} = \alpha_{ij,\ell-1,t}, \ell = 2$ and $\alpha_{ij,\ell,t} = 0, \ell > 2$ and $\alpha_{ij,\ell,t} = \alpha_{ij,\ell,t-2}$ $c_{i,t} = c_{i,t-2}$ $d_{i,t} = d_{i,t-2}$ $r_{i,t} = r_{i,t-2}$
f) One season lag, yearly variation in dem. parameters but constant α	$\alpha_{ij,\ell,t} = 0, \ell > 1$ and $\alpha_{ij,\ell,t} = \alpha_{ij,\ell,t-2}$
g) One season lag, constant dem. parameters but yearly variation in α	$\alpha_{ij,\ell,t} = 0, \ell > 1$ $c_{i,t} = c_{i,t-2}$ $d_{i,t} = d_{i,t-2}$ $r_{i,t} = r_{i,t-2}$
h) One season lag, yearly variation in dem. parameters and α	$\alpha_{ij,\ell,t} = 0, \ell > 1$

Appendix 2. AIC testing of time lags and interannual variability.

Table 3A2.1. Testing models with different time lags. For each species, the model with the asterisk is the best model (lowest AIC). ΔAIC indicates the difference in AIC between the models. Degrees of freedom (df) is the number of parameters.

	Summer		Fall/spring	
	df	ΔAIC	df	ΔAIC
Carex				
No lag	10	86.5	10	67.5
One season lag	15	1.4	15	0.0*
One year lag	15	29.6	15	52.8
One season and one year different parameters	20	4.0	20	4.2
One season and one year same parameters	15	0.0*	15	9.6
Danthonia				
No lag	10	44.0	10	2.5
One season lag	15	0.0*	15	0.5
One year lag	15	33.4	15	3.8
One season and one year different parameters	20	7.0	20	5.7
One season and one year same parameters	15	12.3	15	0.0*
Schizachyrium				
No lag	10	4.0	10	18.7
One season lag	15	0.0*	15	0.0*
One year lag	15	7.6	15	13.2
One season and one year different parameters	20	6.1	20	6.0
One season and one year same parameters	15	4.6	15	1.8
Hieracium				
No lag	10	3.0	10	9.7
One season lag	15	0.0*	15	0.7
One year lag	15	7.3	15	13.6
One season and one year different parameters	20	7.5	20	5.9
One season and one year same parameters	15	2.6	15	0.0*

Table 3A2.2. Testing yearly variation in demographic parameters (*c, r,* and *d*, abbreviated dem.) and/or interaction coefficients (α's). For each species, the model with the asterisk is the best model (the one with lowest AIC). ΔAIC indicates the difference in AIC between the models. Degrees of freedom (df) is the number of parameters.

	Summer		Fall/spring	
	df	ΔAIC	df	ΔAIC
Carex				
Constant dem. and α	15	42.7	15	0.0*
Variable dem.	21	0.0*	21	4.2
Variable α	35	61.6	35	22.2
Variable dem. and α	41	29.1	41	28.3
Danthonia				
Constant dem. and α	15	23.3	15	70.9
Variable dem.	21	0.0*	21	0.0*
Variable α	35	25.0	35	61.1
Variable dem. and α	41	13.8	41	14.5
Schizachyrium				
Constant dem. and α	15	21.7	15	12.1
Variable dem.	21	0.0*	21	14.1
Variable α	35	43.8	35	0.0*
Variable dem. and α	41	26.2	41	7.2
Hieracium				
Constant dem. and α	15	4.2	15	35.7
Variable dem.	21	0.0*	21	0.0*
Variable α	35	20.6	35	49.2
Variable dem. and α	41	23.5	41	12.5

Appendix 3. Supplementary technical methodology

Global maxima optimization strategy

To ensure that we found global maxima, we took the models from summer and fall/spring with variable demographic parameters and constant interaction coefficients and used a multistart, multistep optimization strategy with 10,000 starts, evaluated the log-likelihood, then selected the top 2% and optimized with a low tolerance (0.01), then selected 20% and optimized with a high tolerance (1e-8). For all species in both seasons, 80% of the optimizations converged to the single global maximum; 20% of the optimizations did not converge due to the wide range of starting values and had lower log-likelihood values (by an average of 9-72 log-likelihoods units).

Univariate profiling

Because parameters may be highly correlated, we used univariate profiling to test how variation of a single parameter affected estimation of other parameters. Specifically we wanted to ensure that variation of a single interaction coefficient within its 95% confidence limits did not change the sign of other interaction coefficients (so that interpretation of the sign of coefficients in terms of competition or facilitation is valid). For all species, using the models for summer and fall/spring with variable demographic parameters and constant interaction coefficients, we constructed univariate profiles along the lagged conspecific interaction coefficient. None of the lagged conspecific interaction coefficients changed sign within their own 95% confidence limits, and likewise none of the important interaction coefficients included in the best models (those listed in Table 3.2) changed sign as the lagged conspecific interaction coefficient varied.

Appendix 4. Standard errors for parameter estimates.

Table 3A4.1. Summer and fall/spring interaction coefficients (per capita effect of species in columns on species listed in rows) with standard errors in parentheses for models without time lags. Estimates are the same as those in Table 3.1. Standard errors (estimated by the quadratic approximation) are shown in parentheses below. Interaction coefficients in bold indicate conspecific interactions; blank cells indicate that the interaction coefficient was not included in the best model (i.e. it is zero). The summer transitions are from three years, summers 2, 3, and 4. The fall/spring transitions are also from three years, fall/spring 1, 2, and 3. These transitions are from the same years as in the lagged models (Tables 3.2 and 3A4.2) to allow comparison. All summer models have variable demographic parameters. In fall/spring models, *Carex* and *Schizachyrium* have constant demographic parameters, and *Danthonia* and *Hieracium* have variable demographic parameters.

		Interaction coefficient				
		C	D	S	H	L
Summer	C	**0.012**	-0.006			-0.007
		(0.009)	(0.007)			(0.008)
	D	0.028		0.032	0.027	0.009
		(0.017)		(0.016)	(0.047)	(0.028)
	S	0.010	-0.006	**-0.020**		-0.070
		(0.025)	(0.013)	(0.009)		(0.003)
	H	0.053	-0.016		**-0.135**	-0.261
		(0.055)	(0.028)		(0.035)	(0.117)
Fall/spring	C	**-0.029**	-0.019	-0.020	-0.005	-0.010
		(0.011)	(0.009)	(0.017)	(0.070)	(0.009)
	D		**-0.013**	0.016	0.103	-0.023
			(0.004)	(0.020)	(0.119)	(0.025)
	S	-0.071	-0.007	**-0.073**	-0.267	-0.021
		(0.030)	(0.015)	(0.011)	(0.227)	(0.026)
	H	-0.114	-0.023	-0.094	**-0.156**	-0.118
		(0.055)	(0.041)	(0.093)	(0.078)	(0.084)

Table 3A4.2. Summer and fall/spring interaction coefficients (per capita effect of species in columns on species listed in rows) with standard errors in parentheses for models with one season time lags. Estimates are the same as those in Table 3.2. Standard errors (estimated by the quadratic approximation) are shown in parentheses below. Interaction coefficients in bold indicate conspecific interactions; blank cells indicate that the interaction coefficient was not included in the best model (i.e. it is zero). All summer models have variable demographic parameters. In fall/spring models, *Carex* and *Schizachyrium* have constant demographic parameters, and *Danthonia* and *Hieracium* have variable demographic parameters.

		Interaction coefficient									
		C	D	S	H	L	C lag	D lag	S lag	H lag	L lag
Summer	C	**-0.071**		-0.035			**0.117**	-0.007	0.043	-0.045	
		(0.013)		(0.022)			(0.013)	(0.009)	(0.023)	(0.065)	
	D	0.025	**-0.030**	0.047			*0.008*	**0.044**	-0.028	0.115	0.030
		(0.023)	(0.005)	(0.023)			(0.025)	(0.006)	(0.027)	(0.096)	(0.020)
	S			**-0.040**	0.121	-0.056			**0.035**	-0.306	
				(0.012)	(0.192)	(0.030)			(0.013)	(0.418)	
	H		-0.037		**-0.185**	-0.215		0.047		**0.302**	
			(0.051)		(0.038)	(0.117)		(0.062)		(0.074)	
Fall/ spring	C	**-0.178**				0.009	**0.166**	-0.017	-0.011		-0.021
		(0.018)				(0.019)	(0.016)	(0.009)	(0.013)		(0.019)
	D		**-0.033**	0.032				**0.024**	-0.012	0.094	
			(0.007)	(0.036)				(0.006)	(0.027)	(0.071)	
	S	-0.060	-0.006	**-0.124**					**0.044**	-0.164	
		(0.030)	(0.015)	(0.015)					(0.009)	(0.160)	
	H	-0.089		*-0.085*	**-0.272**	-0.118				**0.128**	0.143
		(0.054)		(0.092)	(0.083)	(0.104)				(0.033)	(0.125)

Table 3A4.3. Demographic parameters for the different species in summer and fall/spring with standard errors in parentheses. Values are the same as those in Table 3.3. Standard errors (estimated by the quadratic approximation) are shown in parenthesis. In some cases, the model with no long-distance colonization ($c = 0$) did best, and when c was included it was estimated to be approximately equal to 0; so no standard error is shown. For each species, parameters are from the best model by AIC, so some have variable and some have constant demographic parameters. When three parameters are present, they correspond to summer 2, 3, and 4, and fall/spring 1, 2, and 3.

	Growth rate, *r*		Short-distance colonization rate, *d*		Long-distance colonization rate, *c*	
	Summer	Fall/spring	Summer	Fall/spring	Summer	Fall/spring
Carex	-0.2580 (0.0418)	0.0587 (0.0383)	0.1817 (0.0255)	0.1698 (0.0158)	0.0351 (0.0131)	0.1084 (0.0103)
	-0.1203 (0.0358)		0.1346 (0.0182)		0.0084 (0.0094)	
	-0.1178 (0.0334)		0.1196 (0.0130)		0.0056 (0.0051)	
Danthonia	-0.2167 (0.0452)	0.1760 (0.0439)	0.1409 (0.0243)	0.1835 (0.0229)	0.0030 (0.0013)	0.0005 (0.0005)
	-0.1102 (0.0412)	0.3125 (0.0427)	0.0738 (0.0149)	0.1608 (0.0230)	0.0011 (0.0008)	0.0110 (0.0025)
	-0.1105 (0.0443)	0.4176 (0.0432)	0.0388 (0.0088)	0.1538 (0.0229)	0.0015 (0.0009)	0.0224 (0.0039)
Schizachyrium	-0.0989 (0.0640)	0.5015 (0.0496)	0.2924 (0.0389)	0.2073 (0.0164)	0.0007 (0.0005)	0.0004 (0.0002)
	-0.3049 (0.0623)		0.1650 (0.0273)		0.0000	
	-0.2798 (0.0643)		0.0968 (0.0216)		0.0004 (0.0004)	
Hieracium	-0.3124 (0.1497)	0.6746 (0.1424)	0.1901 (0.0424)	0.1410 (0.0374)	0.0000	0.0013 (0.0007)
	-0.6448 (0.1681)	0.6701 (0.1472)	0.1108 (0.0399)	0.1367 (0.0366)	0.0000	0.0003 (0.0003)
	-0.1977 (0.1523)	1.2094 (0.1511)	0.0801 (0.0258)	0.2999 (0.0589)	0.0000	0.0056 (0.0014)

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CHAPTER IV

A test of conspecific and heterospecific interactions in a dry perennial grassland

Abstract

A fundamental requirement for most models of local stable coexistence is that intraspecific interactions are more negative than interspecific interactions. Both classic competition experiments and plant-soil feedback experiments have addressed this question, but they have found contradictory results: competition experiments tend to find competitive hierarchies, whereas plant-soil feedback experiments often find evidence that intraspecific interactions are more negative than interspecific interactions, i.e., negative feedbacks. An approach that could explain this is to measure the intermediaries, such as nutrients, light, or soil microbes, thought to be important in the interaction. In the present study, we use this approach to test conspecific and heterospecific interactions in a field experiment in a dry sand prairie in Michigan. We concentrate on three of the dominant species in the system, *Carex pensylvanica*, *Danthonia spicata*, and *Hieracium piloselloides*. Using a transplant experiment, we ask whether plants perform best in natural field monocultures of conspecifics, heterospecifics, or no neighbor plots. We also measure abiotic environmental characteristics associated with each of these monoculture types to determine if species create different microenvironments, and then we relate them to plant performance to test whether performance can be explained by the aspects of the environment. We hypothesize that plants will create competitive hierarchies because our

experimental design is most closely related to classic competition experiments. Interestingly, transplant biomass was lower in conspecific monocultures compared to heterospecific or no neighbor plots, thus producing negative feedbacks. Plants tended to perform best in no neighbor plots, suggesting that competition, not facilitation, dominates even in this fairly stressful, xeric system. For two of the three species, the effects of neighbors are likely due to reduction of light and soil nitrate, because these soil properties were positively correlated with transplant biomass. These results suggest that combining field transplant experiments with explicit measurement of the environment is successful in determining net interactions that are occurring in plant communities and uncovering mechanisms through which plants interact.

Introduction

A fundamental requirement for most models of local stable coexistence is that intraspecific interactions are more negative than interspecific interactions. This is true for classic ecological theory, namely the Lotka-Volterra competition model, as well as more recent models of coexistence by niche partitioning such as mechanistic consumer-resource models, Janzen-Connell effects and the natural enemies hypothesis, and, over long time periods, the storage effect. In all of these models, formulated at the population level, species compete more strongly with conspecifics than heterospecifics. Despite the importance of this condition for coexistence, few empirical studies in plants test explicitly whether intraspecific competition is stronger than interspecific competition (Silvertown 2004), even though much research from many different areas in ecology has investigated plant interactions at least at the individual level.

It has been thoroughly documented that both competitive and facilitative interactions are important to individual plant performance. Evidence comes from a variety of subdisciplines in ecology: the extensive experimental literature on plant competition both in the field and in pots (Goldberg and Barton 1992, Gurevitch et al. 1992, Keddy 2001), the facilitation literature about the importance of nurse plants in harsh environments (Niering et al. 1963, Bertness and Callaway 1994, Callaway and Walker 1997), the succession literature stressing facilitative effects of early successional plants and competitive dominance of late successional species (Connell and Slatyer 1977, Walker and Chapin 1987, Tilman 1990), and the plant-soil feedback literature (Bever et al. 1997, Bever 2003). However, it is much less clear how individual interactions affect community dynamics and, specifically, coexistence. Many of the studies in the areas mentioned above cannot address coexistence because they do not compare both intra- and inter- specific effects. For example, facilitation research tends to focus only on interspecific effects, such as the effects of shrubs on understory plants and vice versa. The succession literature often focuses on unidirectional effects of early successional species on late successional ones. Many field competition experiments examine the effect of the entire plant community of competitors on individual species but do not measure pairwise interactions.

Pairwise competition designs, often in pots or common garden experiments, and plant-soil feedback experiments are the best suited to address the question of coexistence, because they are often performed with factorial designs including both intra- and inter-specific interactions. These two types of studies both measure net pairwise interactions among plants; however, they incorporate different interaction intermediaries (Fig. 4.1).

Competition experiments assume resource uptake is the mechanism of plant interactions; thus in pairwise competition experiments, species are grown together with either conspecific or heterospecific competitors. Feedback experiments focus on soil microbial communities as intermediaries, such as pathogens and mycorrhizae. In feedback experiments, soils are first "cultivated" by different species, then those individuals are removed, and new plants are grown in the cultivated conspecific and heterospecific soils. Although these two types of experiments are designed to test different intermediaries, the plants in competition experiments are likely also affecting each other through modification of the soil microbial community; and in feedback experiments the "cultivating" species could reduce nutrients or influence nutrient cycling rates and thereby affect the subsequent performance of the target species via those mechanisms.

Interestingly, pairwise competition experiments and feedback experiments have found contradictory results. Both field and greenhouse competition experiments tend to find either competitive hierarchies or no pattern in the relative strength of conspecific and heterospecific competition (Keddy and Shipley 1989, Goldberg and Barton 1992, Gurevitch et al. 1992, Shipley and Keddy 1994, Goldberg 1996). Plant-soil feedback experiments, however, often find evidence for negative feedbacks; that is, effects from conspecific soil are more negative than effects from heterospecific soil (Kulmatiski et al. 2008). These contradictory results suggest that the presence (or absence) of live neighbor plants critically influences the outcome of plant interactions. Recent feedbacks studies have shown that adding direct resource competition with live plants to microbial feedbacks can change the net magnitude and direction of plant effects (Casper and Castelli 2007, Kulmatiski et al. 2008).

An approach that could account for the results of both competition and feedback experiments would be to explicitly measure the intermediaries through which the interactions are thought to occur (Goldberg 1990). Some studies have related abiotic or biotic characteristics of the environment to plant performance to start to tease apart which intermediaries may be important in plant interactions (Foster and Gross 1997, Reynolds et al. 1997, Holzapfel and Mahall 1999, Fargione et al. 2003, Bezemer et al. 2006, Casper et al. 2008); however, these environmental characteristics are often not measured in pairwise competition and feedback studies.

In this study, we compare the strength of conspecific and heterospecific interactions among four species in a dry sand prairie system. Using a field transplant experiment, we measure plant performance with conspecific, heterospecific, and no neighbors (a in Fig. 4.1). This design is most similar to competition experiments, however, the use of natural neighborhoods in the field incorporates neighbor effects on both resources and soil biota. We also measure the abiotic environmental characteristics associated with each of these neighborhoods in natural field monocultures to determine whether species differentially affect the abiotic environment (b in Fig 4.1). To address the responses of species to the environment (c in Fig 4.1), we combine the data sets in (a) and (b) and relate transplant performance to the environmental characteristics in the different neighborhood types using cross-species correlations. This will indicate which aspects of the environment explain plant performance and thus may act as intermediaries in the species interactions. Because our experiment contains live neighbors, we hypothesize that plants in our system will generate competitive hierarchies, consistent with results from the competition literature. Due to the dry, nutrient poor conditions in the sand prairie, we focus on abiotic environmental characteristics such as nutrients, moisture, and light since they will be most limiting, and hypothesize that these will be important intermediaries in plant interactions.

Methods

Study site and species

Field work was carried out in a native grassland in the dry sand prairie of the northern lower peninsula of Michigan near the city of Indian River (latitude 45°23'26"N, longitude 84°35'41"W). Dry sand prairie occurs throughout the Lower Peninsula of Michigan on glacial outwash plains and is characterized by excessively well-drained, sandy soil (Albert 1995) that is very nutrient poor. Dry sand prairie is often interspersed with jack pine barrens, and our study site is a patchy mosaic of grassland, shrub, and jack pine (*Pinus banksiana*) and red pine (*Pinus resinosa*).

The study included the four dominant herbaceous species in the system, which together make up over 90% of the stems (E. C. Farrer, *unpublished data*): *Carex pensylvanica*, *Danthonia spicata*, *Schizachyrium scoparium*, and *Hieracium piloselloides*; nomenclature follows Voss (1972, 1984, 1997). The first three are dominant graminoids native to grasslands and open canopy habitats throughout North America and are characteristic of dry sand prairie (Kashian et al. 2003, Kost et al. 2007). *Hieracium piloselloides* is an exotic from Europe, however it tends not to be invasive and is the rarest of the four species. We also include *Cladina spp.* (reindeer lichen) as a neighbor type in our study; reindeer lichens are dominants in boreal systems and are important components in this system occurring at about 30% cover.

Transplant experiment

The transplant experiment was carried out in natural monoculture plots, which were defined as areas of at least 9 × 9 cm dominated by bare soil or one of the five neighbor types (lichen, *Carex*, *Danthonia*, *Hieracium*, and *Schizachyrium*). Each natural monoculture plot received one transplant, so one replicate of this experiment consisted of 24 natural monoculture plots (4 target species × 6 neighbor types = 24 plots). Each replicate was located in a block of area 2 × 5 m. Ten replicate blocks were arranged continuously in a 20 × 5 m transect in the study site.

Each transplant consisted of a clone of three connected ramets, although for *Hieracium* the ramets were not necessarily still connected because the rhizomes decay quickly and break easily. Transplants were planted as a clone to allow for integration among ramets, which has been found to be important for clonal spread (Fischer and van Kleunen 2002). Adult ramets were used rather than seedlings, because seedling recruitment is low in this dry system (E.C. Farrer, *personal observation*). Transplants were dug up from the study site, their roots were washed to remove soil, and aboveground litter was removed. Rhizomes differed slightly in initial length, which was unavoidable to obtain a sufficient sample of three connected ramets (typical range 1 to 3 cm). Transplants were kept in water for a maximum of 2 days until planting.

Transplants were planted in the neighborhoods from May 25-28 2007. Those that died within the first three weeks after transplanting were replaced. Transplants were watered periodically (approximately twice a week) throughout June and July 2007 to aid in establishment.

Plots were harvested after two growing seasons in Aug 13-18 2008. All neighbor species' stems in the 9 × 9 cm plots were counted and clipped for aboveground biomass and litter mass was also collected. The target stems were counted, and height and number of leaves of each stem was measured. The 9 × 9 block of soil was then harvested to a depth of approximately 20 cm and was frozen until roots and rhizomes of the target plant could be sorted. Noticeably dead parts of target rhizomes (those that were soft and decomposing) were separated out and not included in rhizome biomass. All samples were dried at 55° C and weighed.

Statistical analyses*: *net interactions. *Schizachyrium* was not included as a target species in any analyses because its survival was so low (8 out of the original 60 transplants survived through the second summer).

Three measures were used to describe performance of the *Carex*, *Danthonia*, and *Hieracium* transplants in the different backgrounds: survival, biomass of surviving transplants (shoot + root + rhizome mass of only transplants that survived), and total performance (shoot + root + rhizome mass of transplants that survived and zero for transplants that did not survive). For means for each of these performance measures in each treatment combination, see Appendix 1.

The effect of target species, neighbor type, and their interaction on survival was analyzed by a generalized linear model with binary error distribution and a logit link function (Proc GLIMMIX in SAS, SAS 9.2 SAS Institute, Cary, North Carolina, USA). Performance in bare plots was not used in the analysis of survival, so that it is similar analytically to the analysis of biomass and suvival+biomass (see below), however, the survival of *Carex*, *Dathonia*, and *Hieracium* in bare plots were very similar to each other (*Carex* 0.6, *Dathonia* 0.5, and *Hieracium* 0.6), so this is unlikely to have a strong effect on the analysis. The Gauss-Hermite quadrature method was used for likelihood approximation, and Wald χ^2 tests were used for testing of significance of fixed effects (Bolker et al. 2009). Block was included as a random effect in all models. We tested two different models. First, neighbor type was classified by species with five different levels (lichen, *Carex*, *Danthonia*, *Hieracium*, *Schizachyrium*). Second, neighbor type was classified with two levels, conspecific and heterospecific. Data were slightly underdispersed (Pearson χ^2 /df = 0.98 and 0.90, respectively) but we kept the dispersion parameter equal to 1, making this test more conservative.

For biomass and total performance, relative performance was calculated by a log response ratio comparing the biomass or total performance in a given neighbor type (*Carex, Danthonia, Hieracium, Schizachyrium*, lichen) to their mean performance in bare plots: lrr=ln(performance$_{,C,D,H,S,orL}$/mean performance$_{bare}$). This standardizes the species responses to their performance with no neighbors (i.e. in bare plots) so that responses can be compared among target species. We standardized each sample to the mean no-neighbor performance because of mortality of some transplants in no neighbor plots. For total performance, the analysis was performed on the ln(performance$_{,C,D,H,S,orL}$/mean performance$_{bare}$+1) in order to avoid taking the log of zero when any transplant died. The effect of target species, neighbor species, and their interaction on biomass and total performance log response ratios were analyzed using linear mixed models (Proc MIXED in SAS). Block was used as a random effect in all models. We used a Kenward-Roger approximation to adjust degrees of freedom in the mixed model F tests (Littell et al.

2006). We checked for normality of residuals visually with normal probability plots of residuals and predicted values, and homogeneity of variances with Levene's test. When Levene's test indicated heteroscedasticity, we modeled heterogeneous variances for target only, neighbor only, and both target and neighbor species and used AIC to choose the best model (West et al. 2007). Similar to the survival analysis, we tested two different models: first neighbor type was classified by species with five different levels (lichen, *Carex*, *Danthonia*, *Hieracium*, *Schizachyrium*), and second neighbor type was classified with two levels, conspecific and heterospecific.

To visualize the effects of different neighbors on survival, biomass, and total performance in figures (Fig. 4.1), the log response ratio was used, because positive values indicate facilitation while negative values indicate competition. For survival and total performance, the log response ratio was calculated using means ln(mean performance$_{,C,D,H,S,orL}$/mean performance$_{bare}$), to avoid taking the log of zero. For biomass, the log response ratio was calculated for each plot, and then the mean and the standard error were calculated; thus biomass is the only graph with error bars.

Species effect on the environment

Environmental characteristics thought to be potential intermediaries in plant interactions were measured in June and August of 2007 and 2008 in natural monoculture plots. These natural monocultures were separate from those used in the transplant experiment but located in the same grassland (within 50 m); environmental measurements were not taken from the transplant experiment plots because the plots were small and soil sampling is destructive. Ten replicate 2 × 5 m blocks were laid out in two transects measuring 5 × 40 m (blocks were not continuous). In each block, 5 natural monocultures of each species were flagged; four of these monocultures were used for destructive soil nutrient sampling and one was used for nondestructive repeated measurements of light, temperature, number of stems, and litter and live height/cover.

Nutrient sampling was done in June and August 2007 and 2008 using one month *in situ* buried bag incubations (Eno 1960). On the first of each month, two soil cores (2.54 cm diameter, 10 cm depth) were taken from each natural monoculture plot (6 neighbor types × 10 replicates = 60 natural monocultures) and placed in a polyethylene bag. The aboveground shoot and litter biomass in the area over the cores was clipped, sorted, and dried at 55° C for the June 2007-2008 and August 2007 sampling periods (but not for the August 2008 period due to time constraints). One soil core was put on ice and transported back to the lab for processing, the other was returned to the soil. Incubated samples were retrieved from the field after 28 days. In the lab, soils were sieved (2 mm) and a 20 g subsample was extracted for 1 hour with 40 mL 2M KCl. Extracts were filtered (Whatman GF/F; Whatman, Florham Park, New Jersey, USA) and frozen until colorimetric analysis for NH_4^+ and NO_3^- (Eaton et al. 1995) on a Bran Luebbe autoanalyzer 3 (Hamberg, Germany) and a SmartChem 200 (Westco Scientfic, Inc., Brookfield, CT, USA). Available NH_4^+ and NO_3^- were the values in the initial cores. N mineralization (ug N g^{-2} d^{-1}) was calculated as the increase in NH_4^+ plus NO_3^- over the 28 days; nitrification (ug N g^{-2} d^{-1}) was calculated as the increase in NO_3^- only over the 28 days.

A 10 g subsample was dried at 105°C for wet:dry ratio, and SOM (soil organic matter) was measured by combusting the dried sample for 4 hours at 550°C. Bulk density (g soil/mL) was measured using the August 2007 initial soil cores by subtracting the mass and volume of the coarse fraction from the total core mass and volume. Root and rhizome biomass was also sorted from the August 2007 initial soil cores, dried at 55° C, and weighed, and total C and N of roots was measured by dry combustion on a Perkin Elmer 2400 Series II Elemental Analyzer (Waltham, Massachusetts, USA).

At each sampling period, nondestructive environmental measurements were also taken in the remaining 60 natural monoculture plots in each block. Light penetration through the vegetation and litter was measured as photon flux (μmol s^{-1} m^{-2}) at the soil surface divided by total photon flux above the vegetation using a LI-COR quantum sensor LI-189 (LI-COR, Lincoln, Nebraska, USA). Soil temperature was measured at a depth of 5 cm. Both light and soil temperature measurements were taken within one hour of solar noon. The number of stems was counted within the 9 × 9 cm monoculture plots, and the height and percent cover of live vegetation and litter was measured.

Statistical analyses: species effect on the environment. The effect of neighbor species identity on environmental characteristics (NH_4^+, NO_3^-, N mineralization, nitrification, moisture, SOM, temperature, light) was analyzed using redundancy analysis (RDA) in Canoco 4.0 (ter Braak 1987, ter Braak and Smilauer 1998). The two years of environmental measurements were averaged for each season to accommodate missing data. Neighbor species characteristics (shoot biomass and litter biomass), season, and block were used as covariables in the RDA. Significance of neighbor species identity in explaining environmental variance after accounting for the covariables was tested using Monte Carlo permutation tests within Canoco, with 499 permutations within block, and significance based on the overall (trace) statistic. The initial model included the season ×

neighbor identity interaction, however it explained minimal, although significant, variance (3.6%, *F*=2.054, *P*=0.0040) and was not included in the analysis presented.

A second RDA was performed as above but using only the data from August 2007 because root biomass and C:N was sampled in this time period. This RDA tested the effect of neighbor species identity on the environment, with block, shoot, litter, and root biomass, and root C:N as covariables.

For an alternate analysis of environmental characteristics using linear mixed models see Appendix 2.

Relating net interactions to neighbor effect on the environment

To link target performance to characteristics of the neighbors and their environment, we explored correlations between target performance and neighbor biomass from the transplant experiment and abiotic measurements from natural monocultures. We used Pearson correlations with a two-tailed t test for significance.

Because neighbor aboveground biomass and litter mass in the transplant experiment strongly covaried with background species, the effect of neighbor biomass vs. neighbor species *per se* on target performance unfortunately could not be teased apart in this study. Therefore, we correlated target performance with neighbor biomass and with litter mass separately (with no main effect of neighbor species) to determine if target species responded to the biomass of the neighbor and/or its litter. These cross-species correlations were done on the means of target performance and neighbor biomass and litter in the 6 neighbor types because neighbor characteristics were not measured in plots in which transplants did not survive, making this a conservative test of correlation due to low power (*n*=6).

Eight abiotic environmental characteristics were of interest to relate to target performance: moisture, SOM, NH_4^+, N mineralization, NO_3^-, nitrification, light, and soil temperature. The RDA of the environment showed that these characteristics were clustered in two groups of correlated characteristics that roughly correspond to axes 1 and 2, respectively (Fig. 4.3); group 1 contained NO_3^-, nitrification, light, and soil temperature, and group 2 contained moisture, SOM, NH_4^+, N mineralization. To reduce the number of correlations performed, we chose one characteristic to represent each group, soil temperature and SOM, to correlate with target performance. These correlations were performed on means since environmental measurements were not taken in the transplant experimental plots (*n*=6). Similarly, we could not use RDA sample scores to correlate with target performance because environmental measurements and transplant performance measurements were not paired.

Results

Intraspecific vs. interspecific net interactions

Neighbor identity did not affect the survival of targets, either when classified by neighbor species or by conspecific/heterospecific, but did affect the biomass of surviving transplants and total performance (Table 4.1, Fig. 4.2).

The five neighbor types differentially affected the biomass of the target species (significant target × neighbor interaction) (Table 4.1a). Neighbor species also strongly affected biomass when classified as conspecific/heterospecific, so that all species performed relatively worse with conspecific vs. heterospecific neighbors (Table 4.1b,

Fig. 4.2b). The magnitude of reduction by conspecifics differed among target species (significant target × con/het interaction), for example, *Danthonia* was most negatively affected by conspecifics.

Similarly, target species responded differently to the five neighbor types in their total performance (Table 4.1a). When neighbors were classified as conspecific/heterospecific, target species performed worse with conspecifics, and the extent of this reduction tended to vary among target species (nearly significant interaction, Table 4.1b, Fig. 4.2c). In only two instances was heterospecific competition stronger than conspecific competition, in the effects of *Schizachyrium* and lichen on *Carex* (Fig. 4.2c). Four interactions were facilitative, including the effect of lichen on *Danthonia*, and the effects of *Carex*, *Schizachyrium* and lichen on *Hieracium*.

Species effect on the environment

Species were associated with different suites of environmental characteristics (Table 4A2.2, Fig. 4.3). For example, *Schizachyrium* was associated with high NH_4^+ and SOM, *Hieracium* had high N mineralization rates, *Danthonia* had low light levels, and *Carex* had high light and nitrification rates. Bare and lichen plots also were distinct from plant species backgrounds in that bare plots had very high light and nitrification, and lichen had low N mineralization. Species identity explained a significant proportion of the total variation in environmental characteristics (14.8%, F=8.09, P=0.002) even after the significant effects of shoot biomass and litter mass were taken into consideration (22.5%, F=23.04, P=0.002). Likewise, a second RDA on a reduced dataset from August 2007 showed that species identity explained a significant proportion of the environmental variance (12.3%, *F*=2.41, *P*=0.002) even after accounting for the variation explained by shoot biomass, litter mass, root biomass, and root C:N (31.8%, *F*=6.64, *P*=0.002; data not shown).

Relating net interactions to neighbor effect on the environment

To determine if the negative effects of neighbor species were associated with the biomass of the neighbor or its litter, we investigated correlations among them. *Danthonia* was most negatively affected by neighbor biomass and litter (Table 4.2, Fig. 4.4). *Carex* and *Hieracium* were not strongly affected by neighbor mass, although most correlations were negative (Table 4.2, Fig. 4.4).

Because many of the abiotic environmental characteristics covaried (Fig. 4.3), we chose temperature and SOM to represent suites of environmental characteristics to correlate with target performance. Temperature is correlated with high light, NO_3^-, and nitrification; and SOM is correlated with high moisture, NH_4^+, and N mineralization (Fig. 4.3). The temperature characteristics positively affected *Carex* and *Danthonia* total performance and *Hieracium* survival (Table 4.2, Fig. 4.5). *Danthonia* total performance was negatively affected by the SOM characteristics (Table 4.2, Fig. 4.5).

Discussion

Consistent with classic ecological theory, we found that conspecific interactions tend to be more negative than heterospecific interactions. This is concordant with the results of many feedback experiments, which support negative feedbacks (Kulmatiski et al. 2008), but it is contrary to the vast majority of pairwise competition experiments, which typically find competitive hierarchies among plants (Keddy 2001, Cahill et al. 2008). To take a first step in understanding the underlying mechanisms behind these net interactions, we measured abiotic environmental characteristics in field monocultures of each of the dominant species and found that species are associated with distinct environmental microsites within the grassland. Furthermore, for two species, data suggest that light and nutrient reduction are driving the patterns in net plant interactions. Below we discuss each of the three components of our study, net interaction, effect on the environment, and response to the environment (Fig. 4.1), and implications for this system and plant interactions more broadly.

Intraspecific vs. interspecific net interactions

The presence of neighbors in general facilitated survival of transplants, however the particular identity of the neighbor did not affect survival. In contrast, the effect of neighbors on target biomass and total performance was highly competitive, and conspecific neighbors tended to affect the target most negatively. The finding that neighbors facilitate survival but negatively affect growth is common in many plant studies (Goldberg et al. 1999).

Although consistent with classic competition theory, it is nevertheless surprising that most conspecific interactions are more negative than heterospecific interactions, both in competitive effect and response (i.e., neighbors affect conspecific targets most negatively and targets respond most negatively to conspecific neighbors). This is the result found by most feedback experiments (Kulmatiski et al. 2008), but not pairwise competition experiments which are most similar to our experimental design. Nearly all greenhouse pot competition experiments find competitive hierarchies (Gaudet and Keddy 1988, Keddy and Shipley 1989, Shipley and Keddy 1994, Keddy 2001, Cahill et al. 2008). Field competition experiments tend to also find hierarchies in competitive effect and response or else do not detect any pattern in the strength of intraspecific and interspecific interactions (Goldberg and Barton 1992, Gurevitch et al. 1992, Goldberg 1996). However, a few field experiments have found intraspecific competition to be stronger than interspecific competition for some species pairs in successional grasslands (Fargione et al. 2003, Fargione and Tilman 2005, Dybzinski and Tilman 2007).

A few differences between our study and classic pairwise competition experiments may explain this inconsistency. First, in our study, the neighbor monocultures were chosen to be at maximum natural densities. Some competition studies that find hierarchies, especially hierarchies in competitive effect, are done by manipulating individuals, so that the most competitive species is the one with the greatest individual biomass (Goldberg 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989, Shipley and Keddy 1994, Rösch et al. 1997, Keddy 2001). Our study attempts to add field realism to these pairwise interactions, by allowing species to compete with neighbors at their natural densities; for example the species with the smallest individual biomass, *Danthonia*, had the largest neighbor biomass because it occurs in dense clumps. One caveat to this approach is that we did not measure the shape of the interaction curve, because we restricted neighbor biomass to be near field maximum; so we cannot calculate per-gram effects unless we assume linearity, which is unlikely (Goldberg 1987). Second, our study was carried out over two growing seasons, which is longer than the typical one-season competition experiment. Two growing seasons allows for a reasonable amount of time for plants to partition resources within a growing season. Species differences may be more pronounced over two years because we capture slightly more year-to-year environmental variability. If the storage effect occurs in the grassland, even longer-term competition experiments would be necessary to detect the conspecific < heterospecific pattern. In fact, the other competition studies that have found evidence for niche partitioning have been relatively long term, 3 to 11 years (Fargione et al. 2003, Fargione and Tilman 2005, Dybzinski and Tilman 2007). Lastly, the use of mature connected ramets as transplants in this experiment, rather than seedlings, may detect different types of interactions compared to many competition experiments that measure recruitment phase interactions or ignore clonal growth.

Species effect on the environment

The four plant species created different abiotic environments, which were also distinct from bare or lichen plots. The shoot biomass and litter mass of the neighbor explained some of this variation in the abiotic environment. For example, shoot and litter mass were negatively correlated with light, temperature, NO_3^-, and nitrification; and litter mass was positively correlated with NH_4^+, moisture, and SOM. Live biomass effects on resources such as NO_3^- and light are likely due to direct uptake, because large plants have greater nutrient demand and ability to shade. However, counterintuitively, the two plant species with the greatest live biomass, *Danthonia* and *Schizachyrium*, had the highest NH_4^+ levels. Litter quantity positively affects SOM formation as it is the source of organic matter in the soil (Eviner and Chapin 2003); it also affects N pools and cycling directly through release during decomposition and indirectly through modification of soil temperature and moisture levels (Eviner and Chapin 2003).

However, even after accounting for shoot and litter biomass, a significant amount of the variance remaining was described by neighbor species *per se*. This indicates that other characteristics such as the microbial community associated with each species, differences in plant tissue quality (C:N, lignin, etc.), or leaf architecture are important in driving abiotic environmental differences (Hobbie 1992, Eviner and Chapin 2003). For example, lichen patches had very low SOM, NH_4^+, and N mineralization rates, which has been found in other studies and is likely due to their slow growth rate, lack of belowground structures, and complex secondary chemistry (Sedia and Ehrenfeld 2005). *Danthonia*, *Schizachyrium*, and lichen all exhibited low nitrification rates, which may also be due to litter chemistry (Wedin and Tilman 1990, Eviner and Chapin 2003).

Relating net interactions to neighbor effect on the environment

To take a first step to identify intermediaries that may play a role in net interactions, we explored relationships between target performance and characteristics of the neighbors and their environments. For the target *Danthonia*, both neighbor biomass and litter mass negatively affected performance, while temperature and its correlated abiotic variables (light, NO_3^-, and nitrification) positively affected performance. Light reduction may be driving the pattern of conspecific vs. heterospecific effects for *Danthonia*, because *Danthonia* neighbors had the largest biomass and litter mass, and lowest light levels in the field. *Carex* target biomass showed a threshold effect, that targets were largest in plots with no neighbors but that the presence of any amount of neighbor reduced growth. This could be explained by the lower light and NO_3^- levels in plots with neighbors and is consistent with the positive correlation between *Carex* performance and temperature and its correlated variables (light, NO_3^-, and nitrification). *Hieracium* was not strongly affected by neighbor biomass or environmental characteristics, except that survival was higher in neighborhoods with high neighbor biomass and low temperature suggesting the importance of neighbors in ameliorating the hot temperatures that can occur in dry sand prairie. *Hieracium* likely has the highest susceptibility to drought of all the species, because it has the highest transpiration rates (E.C. Farrer, *unpublished data*). However, neither neighbor nor environmental characteristics could explain the pattern of conspecific competition being greater than heterospecific competition for biomass or total performance of *Hieracium*.

A few competition and feedback studies have measured abiotic characteristics of soils to determine which properties may be intermediaries in feedbacks. These studies have found that certain abiotic characteristics affect target performance, for example nitrate (Reynolds et al. 1997), nitrate and light (Fargione et al. 2003), potassium (Bezemer et al. 2006) or potassium, magnesium, and calcium levels (Casper et al. 2008). However, in these studies, nutrients or light could not explain the pattern of conspecific competition being greater than heterospecific competition for all species pairs, suggesting some other mechanism is also at work.

Similarly, the lack of strong correlation to the abiotic environment especially for *Hieracium* in the present study suggests that species may be responding to soil biota. Species may accumulate species-specific soil pathogens or unfavorable mycorrhizae in the local soil environment, so that conspecific transplants perform worst in conspecific neighborhoods, producing negative feedbacks. Both greenhouse feedback experiments

(Casper et al. 2008, Kulmatiski et al. 2008) and to a lesser extent field experiments (Kulmatiski et al. 2008) have found negative feedbacks dominate; and often certain mycorrhizae (Bever 2002, Klironomos 2002, Casper and Castelli 2007) or fungal pathogens (Van der Putten and Peters 1997, Holah and Alexander 1999, Klironomos 2002) can be identified as important intermediaries.

Competition and feedback studies

The fact that competition experiments find competitive hierarchies while feedback experiments find that conspecific interactions are more negative than heterospecific interactions suggests that net interactions (Fig. 4.1) through resource uptake mechanisms have different outcomes than interactions through soil microbes. This leads to the question of what is the combined net effect of all abiotic and biotic intermediaries in the field, which will be the determinant of population dynamics. Our study attempts to address this by performing a competition experiment in field natural monocultures, which contain both accumulated effects on resources and microbes.

A few other studies have addressed this by explicitly combining competition and feedback experiments. For some species, adding live plant competitors to a feedback experiment does not change the results from soil-only experiments, but for some species competition can outweigh the soil-only feedback (Casper and Castelli 2007). Other studies have found that soil source influences competitive ability for some species (Reynolds et al. 1997, Van der Putten and Peters 1997, Reinhart and Callaway 2006) but not for others (Bever 1994, Reinhart and Callaway 2006). These results suggest that the balance of different intermediaries is idiosyncratic, and cannot be predicted based on a soil-only feedback experiment or a competition-only experiment; sometimes uptake mechanisms may dominate the net interaction while sometimes microbial intermediaries may dominate.

Implications

The results from this study, that conspecific competition is greater than heterospecific competition for the three target species, suggest that niche processes occur in this grassland. These niches may be driven by resource reduction, as in the case of *Danthonia* neighbors reducing light levels, or modification of soil microbial communities. The species could also occupy different temporal niches (e.g., differences in peak flowering time).

This pattern in conspecific and heterospecific competition is predicted for species that stably coexist under classical competition theory. However, coexistence theory is actually based on population level interactions, not individual interactions. The fact that the three species are clonal and were transplanted as clones in this experiment may begin to bridge the gap between population and individual interactions, since at least some of the population growth in this system is via clonal expansion. However, studies of seed germination would be necessary to complement the clonal growth data to understand overall population interactions.

An alternative method of measuring population dynamics is by fitting population dynamic models to long-term survey data to estimate population-level competition coefficients. We used this approach in this same sand prairie system and found similar results: per capita interaction coefficients were more negative for conspecific than heterospecific interactions (E.C. Farrer, D.E. Goldberg, and A.A. King, *in press*). Other studies have used this approach and have found that conspecific interactions are more negative than heterospecific interactions in some grassland communities (Rees et al. 1996, Freckleton et al. 2000, Adler and HilleRisLambers 2008), but not others (Law et al. 1997). It is important to link these model-fitting studies with experiments in the same system not only to validate the results, but to explore the mechanisms through which the interactions occur.

Conclusions

This study demonstrated that net interactions among three dominant dry sand prairie species could be quantified using a field competition experiment, which we are confident measures interactions important in driving community dynamics in the field. By combining a field competition experiment with measurements of abiotic environmental characteristics, we were able to take a first step explaining the interesting result that conspecific competition was stronger than heterospecific competition. The next step would be to quantify the microbial communities associated with each of these species to determine the influence of pathogens or mycorrhizae on net interactions. Linking this field experiment with data driven models based on temporal dynamics that found concordant results suggests that niche processes are likely important to this community.

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Table 4.1. Effects of target identity (*Carex*, *Danthonia*, *Hieracium*) and (a) neighbor identity (lichen, *Carex, Danthonia, Hieracium, Schizachyrium*) or (b) neighbor type (conspecific, heterospecific) on target performance. Numbers for survival are χ^2 values with degrees of freedom in subscript, and numbers for biomass are *F* statistics with numerator and denominator degrees of freedom in subscript. Block is a random variable and the number shown is a *Z* statistic testing whether the variance component is different from zero. Significance is indicated by asterisks (*** *P*<0.001, ** *P*<0.01, * *P*<0.05, † *P*<0.10). Denominator degrees of freedom are not consistent because species had different numbers surviving to include in the biomass statistics and some models included heterogeneous variances for target and neighbor species; denominator degrees of freedom were estimated by the Kenward-Roger approximation.

a)

Variable	Target species	Neighbor identity	Target × neighbor	Block
Survival Binary (yes, no)	3.94_{2}	1.97_{4}	5.87_{8}	0.41
Biomass ln(response ratio)	$0.13_{2,41.4}$	$3.69_{4,42.9}$*	$3.23_{8,49.3}$**	1.34
Total performance ln(response ratio+1)	$5.23_{2,81.3}$**	$1.04_{4,107}$	$2.26_{8,98.2}$*	-0.35

b)

Variable	Target species	Conspecific / heterospecific	Target × con/het	Block
Survival Binary (yes, no)	8.96_{2}*	0.39_{1}	3.94_{2}	0.29
Biomass ln(response ratio)	$1.94_{2,44.8}$	$20.74_{1,50.8}$***	$4.37_{2,45.4}$*	1.40
Total performance ln(response ratio+1)	$3.81_{2,31.3}$*	$7.91_{1,42}$**	$2.96_{2,31.3}$†	-0.93

Table 4.2. Correlations between measures of target performance and neighborhood characteristics. Neighbor biomass and litter mass measurements were from the transplant experiment. Soil temperature and SOM were measured in separate environmental monocultures. Due to covariance among environmental characteristics, temperature represents light, NO_3^- and nitrification, and SOM represents moisture, NH_4^+, and N mineralization. Values are Pearson correlation coefficients for the correlation between the mean target performance and the mean neighborhood characteristics ($n = 6$), $^{**}P<0.01$, $^{*}P<0.05$, †$P<0.10$ (two-tailed test). For *Danthonia*, coefficients in parentheses represent correlations excluding the lichen neighbor type, because it appeared to be an outlier ($n = 5$).

Performance measure		*Carex*	*Danthonia*	*Hieracium*
Survival	Neighbor biomass	-0.39	-0.34	0.73†
	Litter mass	0.12	-0.15	0.24
	Temp (light, NO_3^-, nitrification)	0.41	0.50	-0.87*
	SOM (moisture, NH_4^+, N mineralization)	0.25	-0.40	0.01
Biomass	Neighbor biomass	-0.38	-0.17 (-0.93*)	-0.34
	Litter mass	-0.16	-0.80†	-0.48
	Temp (light, NO_3^-, nitrification)	0.67	0.13 (0.79)	0.29
	SOM (moisture, NH_4^+, N mineralization)	-0.38	-0.76†	-0.21
Total performance	Neighbor biomass	-0.59	-0.26 (-0.95*)	0.18
	Litter mass	-0.03	-0.80†	-0.31
	Temp (light, NO_3^-, nitrification)	0.86*	0.27 (0.91*)	-0.38
	SOM (moisture, NH_4^+, N mineralization)	-0.15	-0.83*	-0.11

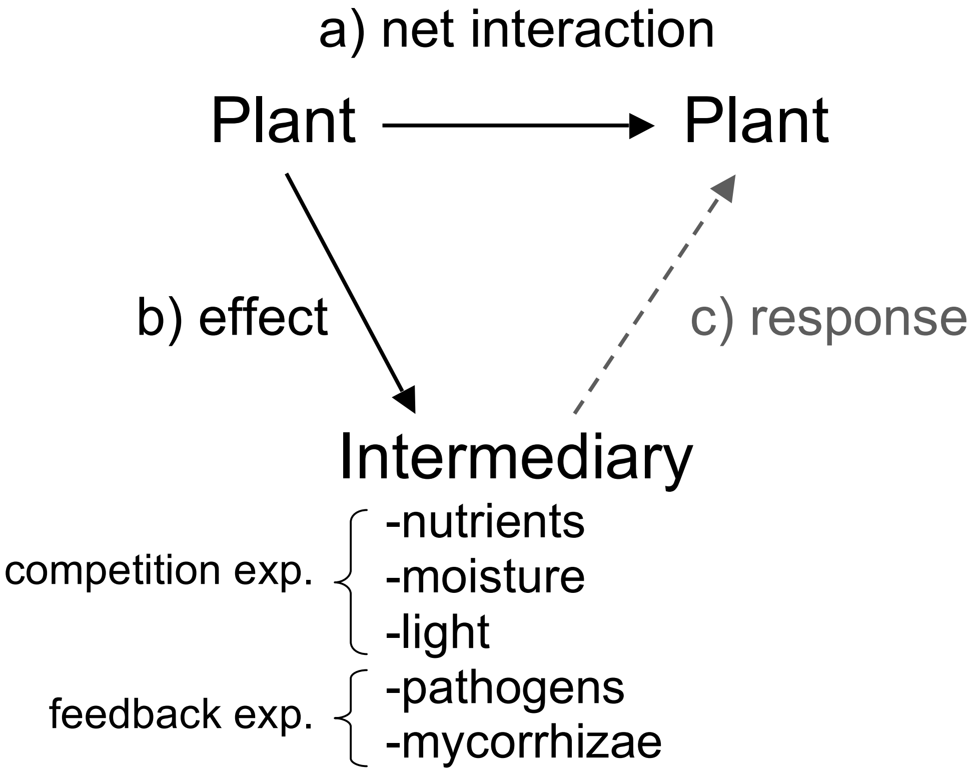
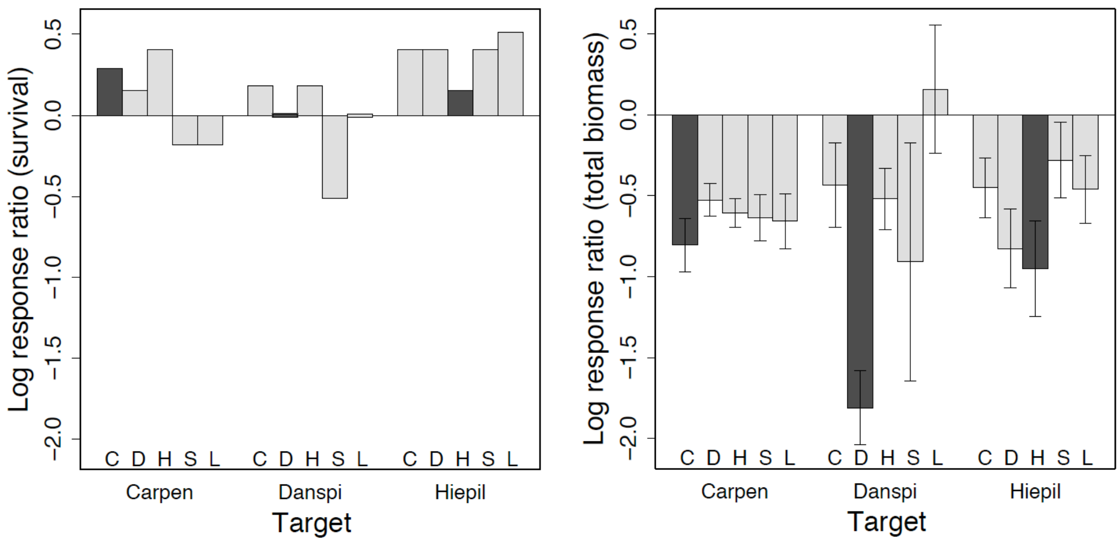


Fig. 4.1. Simple diagram illustrating interactions among plants. Plants primarily interact through modification of the environment or other intermediaries. We measure the net interaction among plants in a transplant experiment (a), and the effect of species on a suite of abiotic environmental properties in field monocultures (b). It is difficult to directly and experimentally measure the response of plants to a wide range of different environmental conditions (c) so we make this link by combining data sets from (a) and (b), and relating the performance of target plants to the environmental characteristics in the different species' neighborhoods.

a) Survival ln(mean/mean)

b) Biomass



c) Total performance ln(mean/mean)

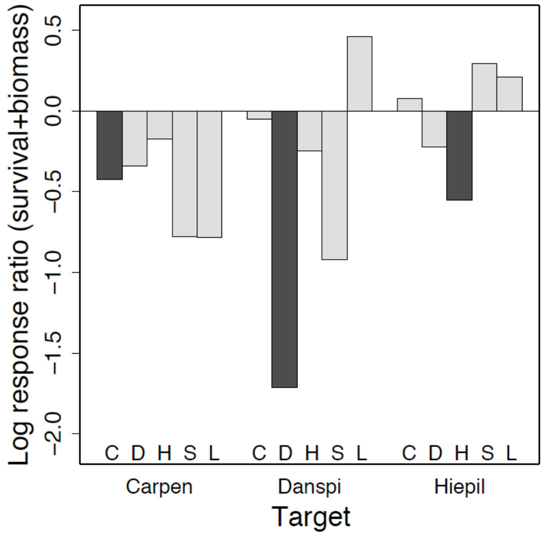


Fig. 4.2. Relative performance of the three target species in different backgrounds for a) survival, b) biomass, and c) total performance data. Relative performance was calculated by a log response ratio of the performance in the three backgrounds to the average performance in bare plots: lrr=ln(performance$_{C,D,H,S,orL}$/performance$_{bare}$). Survival and total performance figures do not have error bars because log response ratios had to be calculated on mean performance (see text). The biomass figure has error bars (± 1 S.E.) because log response ratios were calculated by plot and then averaged. Dark grey bars represent species performance with conspecifics and light grey represents performance with heterospecifics. Abbreviations for the target species are Carpen, *Carex pensylvanica*; Danspi, *Danthonia spicata*; and Hiepil, *Hieracium piloselloides*); abbreviations for background species that are listed along the bottom of each figure are C=*Carex*, D=*Danthonia*, H=*Hieracium*, S=*Schizachyrium*, and L=lichen.

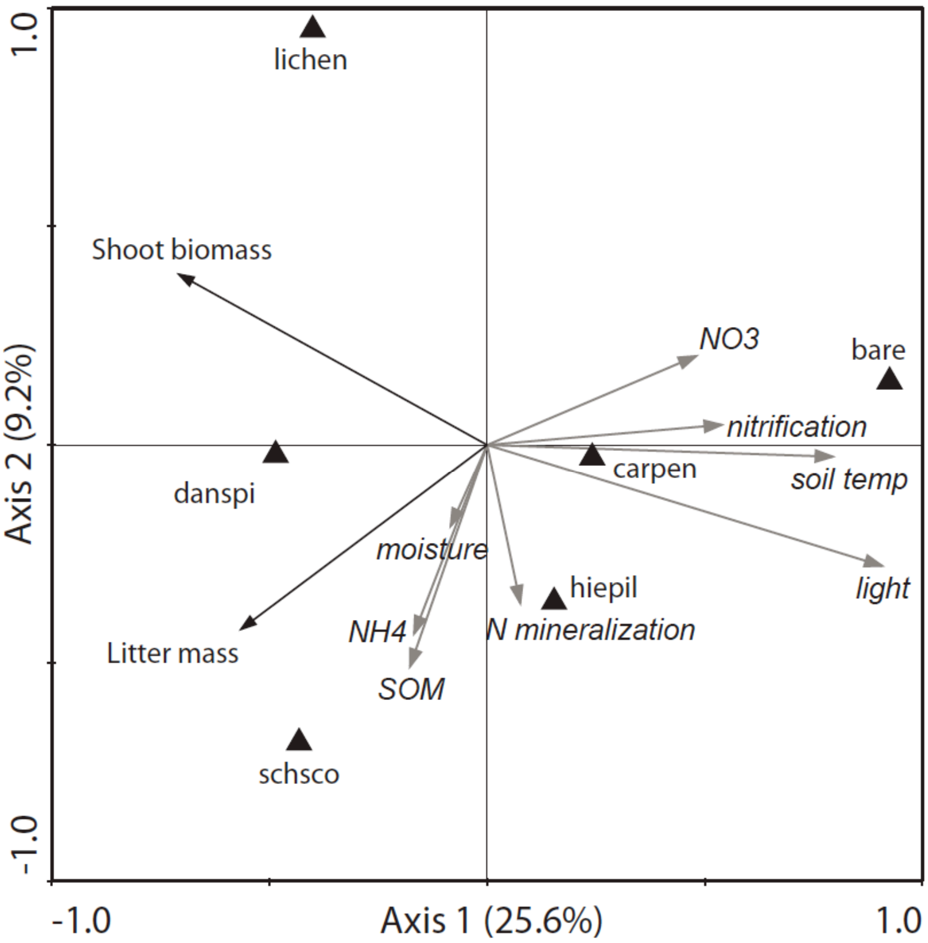
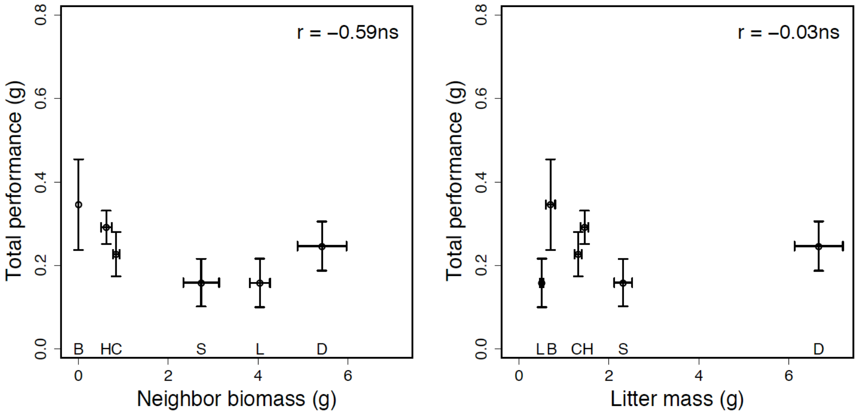
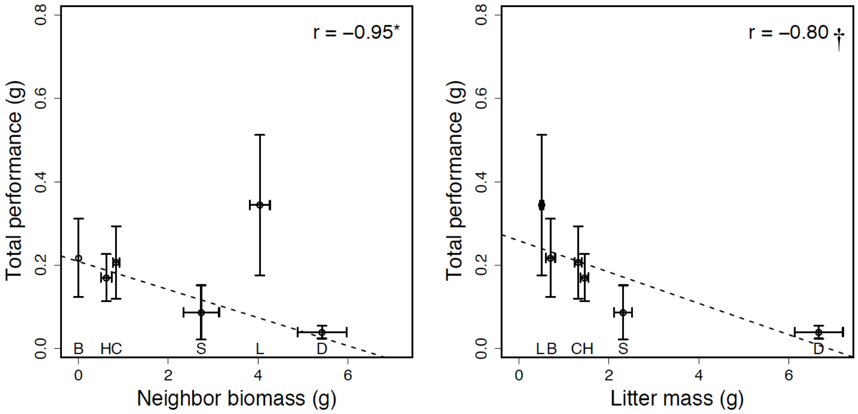


Fig.4.3. Biplot from RDA ordination of the effect of background species identity, shoot biomass, and litter biomass on environmental variables. Axes 1 and 2 explain 25.6% and 9.2% of the total variation, respectively. Block and season were used as covariables in the analysis; block explains 11.0% and season 14.4% of the environmental variation. Shoot and litter biomass explain 22.5% of the environmental variation after accounting for block and season (F=23.04, p=0.0020), and species identity explains an additional 14.8% (F=8.09, p=0.0020). Abbreviations are as follows: carpen, *Carex pensylvanica*; danspi *Danthonia spicata*; hiepil *Hieracium piloselloides*; schsco *Schizachyrium scoparium*. Lichen mass was considered "shoot biomass" in the analysis.

a) *Carex* b) *Carex*



c) *Danthonia* d) *Danthonia*



e) *Hieracium* f) *Hieracium*

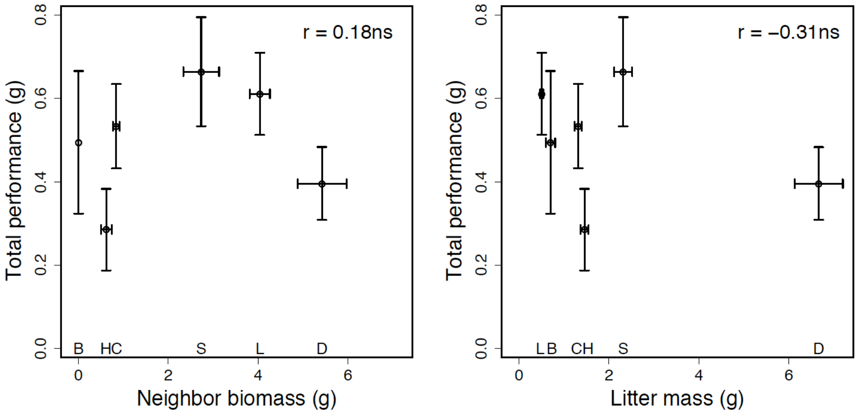
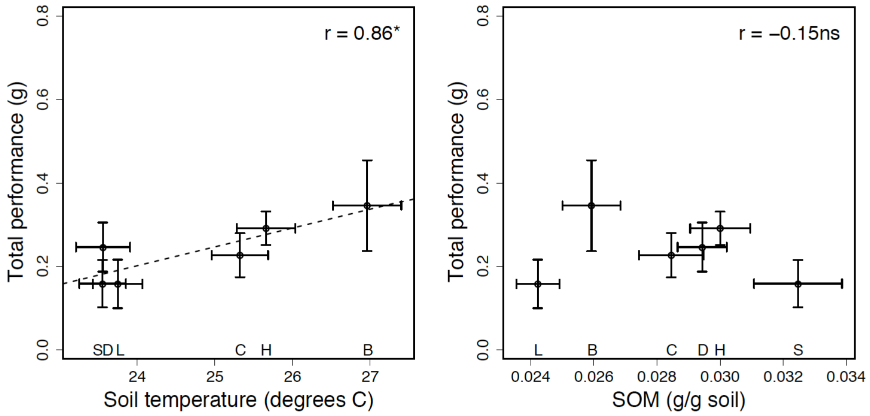
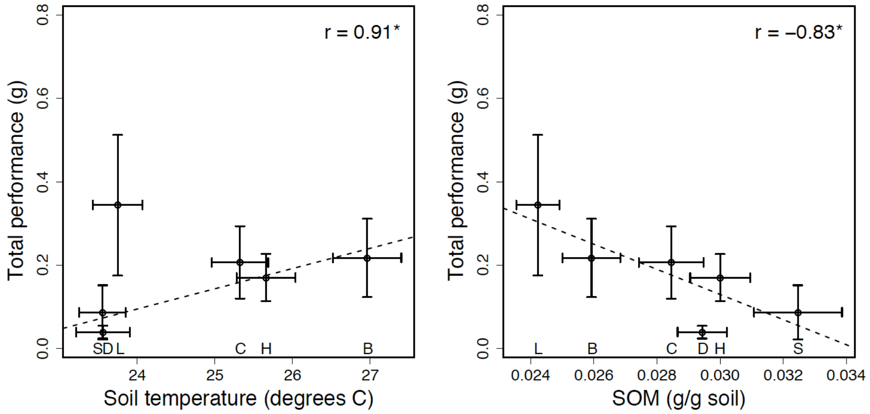


Fig. 4.4. Effect of neighbor biomass and litter mass on target total performance for *Carex* (a, b), *Danthonia* (c, d) and *Hieracium* (e, f). Each point represents mean performance and mean neighbor mass (± 1 S.E.) in one neighbor type; neighbor types are listed along the x axis (B=bare, C=*Carex*, D=*Danthonia*, H=*Hieracium*, L=lichen, S=*Schizachyrium*). Pearson correlation coefficients are shown in the upper right corner and dashed lines indicate a significant or nearly significant correlation (**$P<0.01$, *$P<0.05$, †$P<0.10$, ns = not significant, see Table 4.2); for (c), the correlation excludes the outlier, lichen.



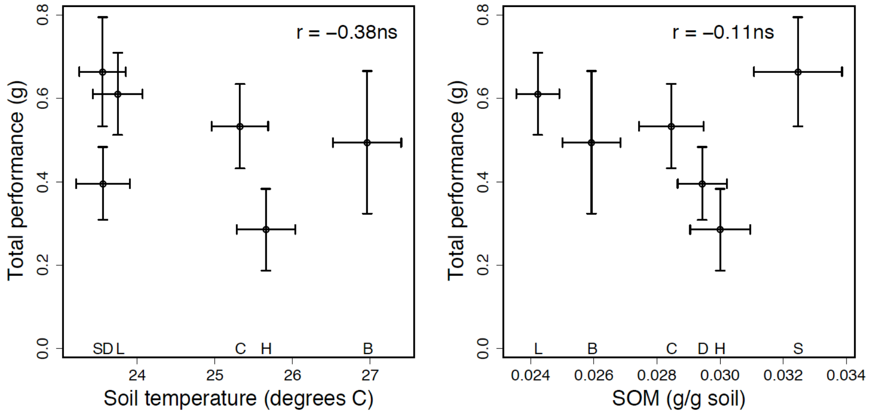
a) *Carex*

b) *Carex*



c) *Danthonia*

d) *Danthonia*

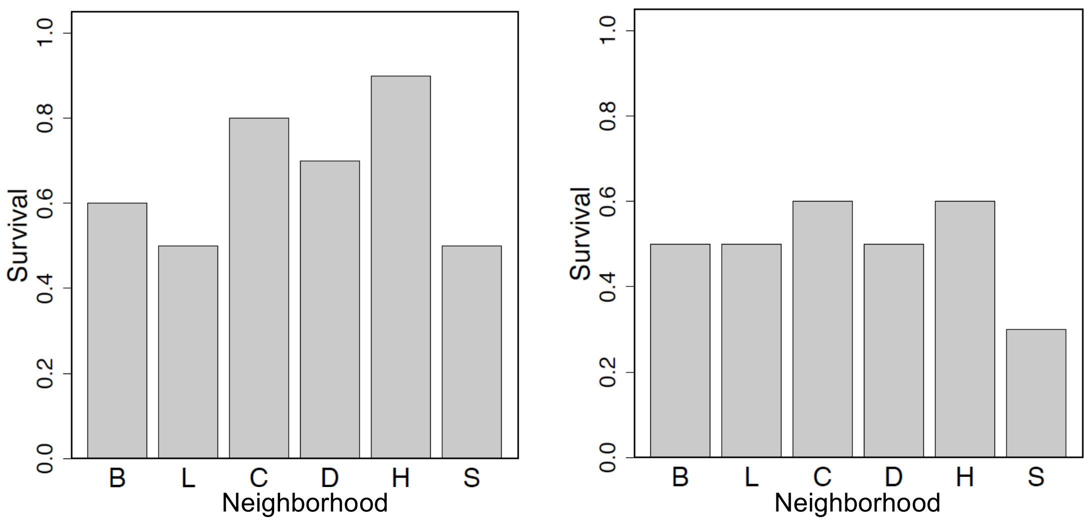


e) *Hieracium*

f) *Hieracium*

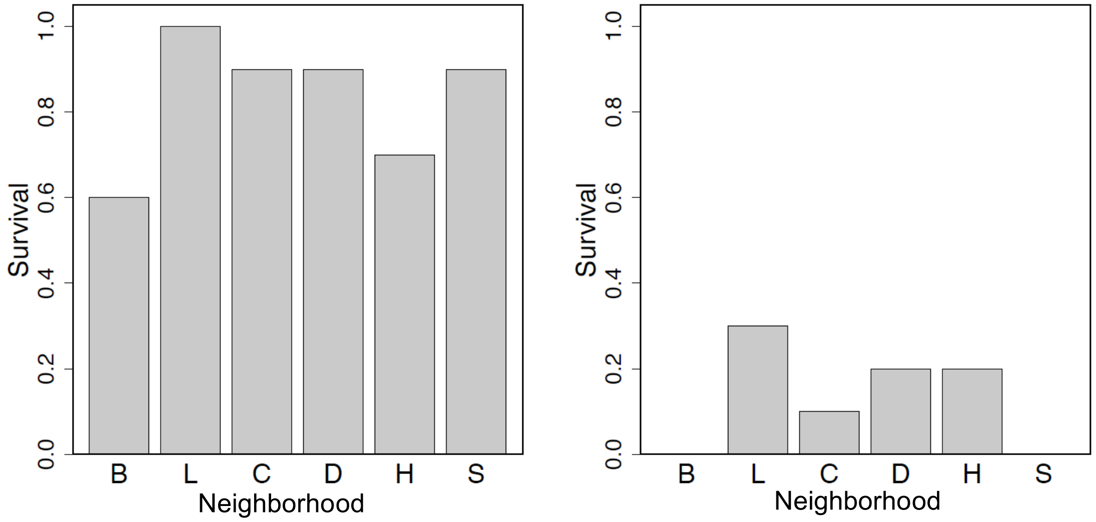
Fig. 4.5. Effect of environment on target total performance for *Carex* (a, b), *Danthonia* (c, d), and *Hieracium* (e, f). Soil temperature was used as a proxy for light, NO_3^-, and nitrification; SOM was used as a proxy for moisture, NH_4^+, and N mineralization. Each point represents means (± 1 S.E.) in one neighbor type; neighbor types are listed along the x axis (as in Fig. 4.4). Pearson correlation coefficients are shown in the upper right corner and dashed lines indicate a significant correlation (***P*<0.01, **P*<0.05, †*P*<0.10, ns = not significant, see Table 4.2); for (c), the correlation excludes the outlier, lichen.

Appendix 1: Means for survival, biomass, and total performance in the six neighborhood types.



a) *Carex*

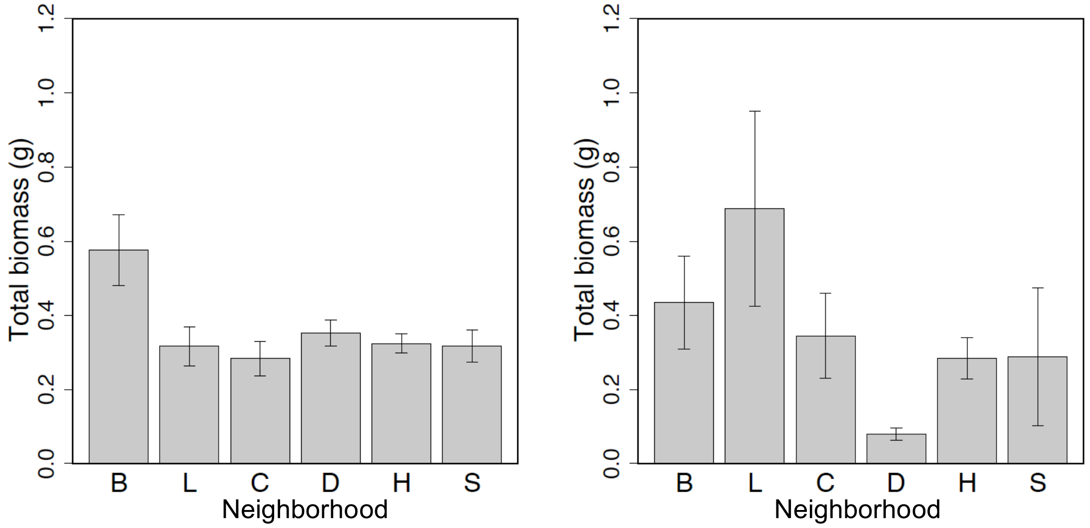
b) *Danthonia*



c) *Hieracium*

d) *Schizachyrium*

Fig. 4A1.1. Survival of the four target species in the six neighborhood types.


a) *Carex*

b) *Danthonia*

c) *Hieracium*

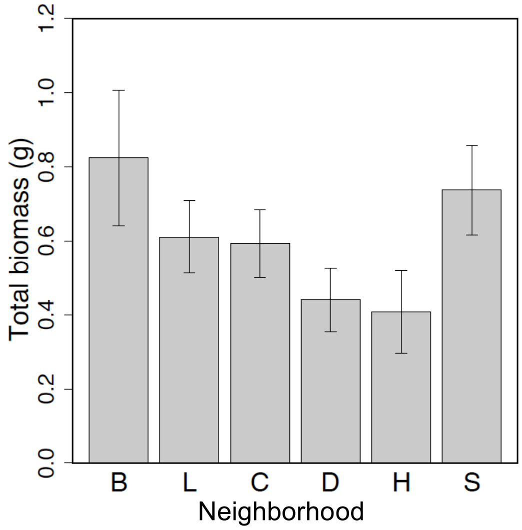
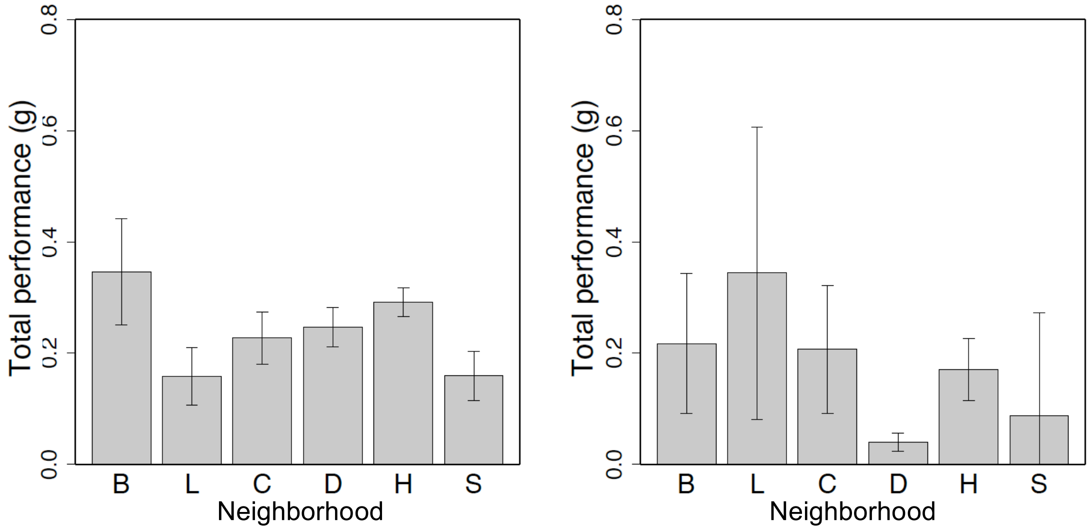


Fig 4A1.2. Biomass (shoot, root, and live rhizome) of each of the three target species in the six neighborhood types.


a) *Carex*

b) *Danthonia*

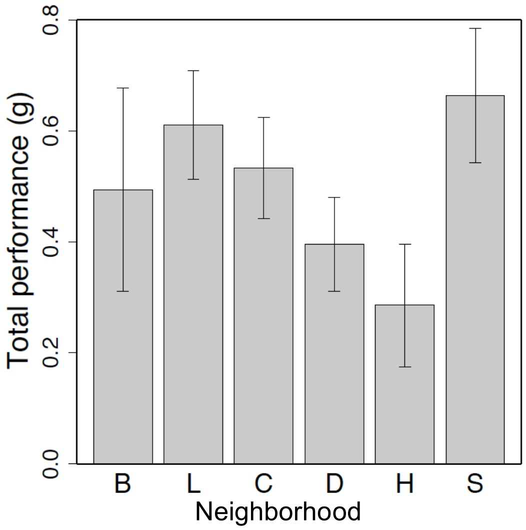

c) *Hieracium*

Fig 4A1.3. Total performance (biomass with zeros for transplants that did not survive) of each of the three target species in the six neighborhood types.

Appendix 2.: Alternate analysis for the environmental data.

Table 4A2.1. Effects of neighborhood type (*Carex, Danthonia, Hieracium, Schizachyrium,* lichen, or no neighbors), season, year, and neighborhood × season interaction on environmental variables. Data were analyzed using linear mixed models (SAS 9.2) and were log transformed if needed to correct for non-normal residuals. Numbers shown for all variables except block are *F* statistics with numerator and denominator degrees of freedom in subscript. Block is a random variable and the number shown is a *Z* statistic testing whether the variance component is different from zero. Significance is indicated by asterisks (*** $P<0.001$, ** $P<0.01$, * $P<0.05$, † $P<0.10$). Numerator and denominator degrees of freedom are not consistent because variables were measured different numbers of times, some models were fit with heterogeneous variances, and a few data points are missing; denominator degrees of freedom were estimated by the Kenward-Roger approximation. Root C:N, root biomass, and rhizome biomass were only measured at one time point, so season, year, and neighborhood × season effects could not be analyzed.

Variable	Neighborhood	Season	Year	Neighborhood × season	Block
NH_4^+	$11.59_{5,218}$***	$5.44_{1,218}$*	$13.53_{1,218}$***	$0.81_{5,218}$	1.32
NO_3^-	$18.73_{5,140}$***	$48.49_{1,140}$***	$1.38_{1,137}$	$3.91_{5,140}$**	1.41
Inorganic N	$6.57_{5,218}$***	$17.25_{1,218}$***	$13.85_{1,218}$***	$1.24_{5,218}$	1.06
N mineralization	$13.37_{5,83.6}$***	$29.58_{1,147}$***	$1.73_{1,161}$	$4.01_{5,83.6}$**	1.77†
Nitrification	$18.37_{5,91.3}$***	$21.55_{1,157}$***	$8.38_{1,105}$**	$1.35_{5,91.3}$	1.73†
SOM	$10.48_{5,218}$***	$3.54_{1,218}$†	$9.74_{1,218}$**	$2.14_{5,218}$†	0.85
Moisture	$4.28_{5,218}$**	$355.05_{1,218}$***	$12.00_{1,218}$***	$1.05_{5,218}$	1.57
Light (no lichen)	$152.99_{4,36.2}$***	$13.08_{1,45}$***	$12.26_{1,49}$**	$10.92_{4,45}$***	-0.79
Temperature	$13.18_{5,42}$***	$275.04_{1,54.3}$***	$315.89_{1,59}$***	$3.03_{5,54}$*	0.99
Root C:N (no bare, lichen)	$3.46_{3,27}$*				-1.55
Root biomass	$12.13_{5,45}$***				-0.35
Rhizome biomass	$86.70_{5,45}$***				-0.97
Litter biomass	$155.57_{5,158}$***	$8.86_{1,158}$**	$2.77_{1,158}$†	$1.99_{5,158}$	1.03
Live biomass	$195.96_{5,158}$***	$7.26_{1,158}$**	$4.62_{1,158}$*	$13.26_{5,158}$***	0.80

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CHAPTER V

Conclusion

Individual plants interact through a variety of different mechanisms, including nutrients, light, and soil microbes, and these interactions can have consequences at the community and ecosystem levels. However, despite the large body of work both at the experimental and theoretical levels, it remains largely untested whether experimentally-measured interactions among individuals drive the large-scale patterns of community structure and dynamics in the field.

In this dissertation, I integrate spatio-temporal field surveys with manipulative experiments within the same system to comprehensively test the importance of plant interactions in driving community dynamics. To understand the mechanisms behind these interactions, I also test many of the intermediaries through which the interactions are thought to occur, such as nutrients, light, and plant litter. I use this framework to test plant interactions and their consequences in two distinct systems, temperate wetlands invaded by hybrid cattail and native dry sand prairie in Michigan. Below I summarize the results from my three primary chapters.

Chapter II. Litter drives ecosystem and plant community changes in cattail invasion. Invaded systems are commonly associated with a change in environment and a decline in native species diversity (D'Antonio and Vitousek 1992, Galatowitsch et al. 1999, Zedler and Kercher 2004); however, many different causal pathways linking these three factors could produce this pattern. In this chapter, I used invaded Great Lakes coastal marshes as a study system to test whether the invasive species itself, *Typha x glauca*, could be driving these changes in ecosystem processes and native species diversity.

In a survey including transects in three marshes, I found that *T. x glauca* was associated with locally high soil nutrients (NH_4^+ and PO_4^{3-}), low light, and large amounts of litter. Also, native diversity, especially that of obligate wetland sedges, rushes, and bulrushes, was highest in areas of shallow litter depth. I then tested whether live *T. x glauca* plants or their litter induced changes in the environment and in diversity with a live cattail / cattail litter transplant experiment. After one year, *T. x glauca* litter increased soil NH_4^+ and N mineralization twofold, lowered light levels, and decreased the abundance and diversity of native plants, while live *T. x glauca* plants had no effect on the environment or on native species. Moreover, *T. x glauca* plants appeared to benefit from their litter, because they were taller when grown in litter plots.

Thus, experimental manipulations of cattail litter produced the same environmental and plant community effects as seen in the large-scale survey. This suggests that *T. x glauca*, through its litter production, can cause the changes in ecosystem processes that we commonly attribute to anthropogenic nutrient loading; and that *T. x glauca* does not displace native species through competition for resources, but rather affects them nontrophically through its litter via light reduction. Because *T. x glauca* plants actually benefited from their litter, this suggests that the invader may produce positive feedbacks and change the environment in ways that benefit itself and promote its own invasion.

Chapter III. Time lags and the balance of positive and negative interactions in driving grassland community dynamics. In order to test whether individual plant interactions and feedbacks have community consequences, it is necessary to first quantify the patterns in population dynamics that occur in the field. Both facilitative and competitive interactions occur simultaneously among plants, and the net balance between them can change over time and among different pairs of species. In this chapter, I used model-fitting techniques (Rees et al. 1996, Law et al. 1997, Freckleton and Watkinson 2001, Adler et al. 2006) to quantify population level interactions among the four dominants in a dry sand prairie. I fit population dynamic models to four years of small-scale spatial data and I included seasonality, interannual variation, and time lags in models to test for patterns in positive and negative interactions. Due to the harsh, hot, dry conditions in this system, I predicted interactions would be largely facilitative (Bertness and Callaway 1994), and because species appear to be coexisting in this system, I expect conspecific interactions to be more negative than heterospecific.

Results indicate that most immediate (direct) interactions among dominant species are actually competitive, although interactions were more facilitative over the drier summer season. Interestingly, lagged density dependence was strong for all species in both seasons; it was positive for conspecific interactions, and both positive and negative for heterospecific interactions. Observed lagged density dependence is likely due to effects from litter and/or effects from past storage in rhizomes. Conspecific immediate and lagged interactions tended to be stronger than heterospecific interactions, suggesting that population dynamics in this community are driven mostly by conspecifics. Moreover, conspecific immediate interactions tended to be more negative than heterospecific interactions, suggesting negative feedbacks occur and stable coexistence though niche mechanisms may be possible for these four species. However this conclusion is tenuous because the conspecific lagged interactions were positive, which may introduce population fluctuations or instability to the system.

Chapter IV. A test of competition and facilitation in a dry perennial grassland. Conspecific and heterospecific interactions in the dry sand prairie were also investigated experimentally in a field competition experiment to determine whether experiments support negative feedbacks. Negative feedbacks are a fundamental requirement for most models of local stable coexistence; however most classic pairwise competition experiments do not find evidence for negative feedbacks, but rather find evidence of competitive hierarchies. In this chapter, I used a field transplant experiment to measure performance of plants with different neighbors, and I related transplant performance to environmental characteristics in natural field monocultures to determine which intermediaries might play a role in the interactions.

Neighbors in general tended to increase transplant survival, but not in a species-specific manner. Plant biomass and combined performance (biomass with zeros when transplants did not survive), however, for the three dominant species was lower with conspecific neighbors compared to heterospecific or no neighbor plots, thus producing negative feedbacks. Plants tended to perform best in bare plots, which suggests that competition, not facilitation, dominates even in this fairly stressful, xeric system. For two of the species, *Danthonia* and *Carex*, transplant performance could be partly explained by neighbor reduction of light and soil nitrate, suggesting these are important intermediaries in the plant interactions. However, *Hieracium* did not correlate with any abiotic soil properties, which indicates that other mechanisms, such as pathogens or mycorrhizae, may play a role.

The results from this experiment are largely consistent with results from the survey in Chapter III. The importance of competition in this system and the pattern that conspecific competition is generally stronger than heterospecific competition suggests that negative feedbacks are driving the community dynamics in the field and that nutrients and light are important intermediaries in plant interactions.

Synthesis. This dissertation illustrates that integrating field surveys with experiments is successful in both uncovering the mechanisms through which plants interact as well as linking individual local interactions with broader scale patterns over space and time. The feedback framework is useful for examining plant interactions because many intermediaries simultaneously influence net interactions in the field. One common theme found in this research is the importance of nontrophic mechanisms, particularly litter deposition, in influencing environmental intermediaries. In two very different systems, litter played a key role in reducing light levels and increasing soil nutrients so that its effect on the interaction was equal to or more important than live plants. This suggests that interactions through litter should not be studied apart from resource uptake, because the combined effects will influence interactions in the field.

Overall, these two very different systems correspond to predictions from existing theoretical and experimental studies that invasive systems exhibit positive feedbacks while native systems exhibit negative feedbacks. It is a step toward understanding how local interactions can contribute to the dominance of invasives and the coexistence of native plants and how the properties of invaded and native systems differ.

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