

The Effects of Nutrient Pulses and Community Diversity
on Invasive Plant Success in Virginia

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Abstract

What makes a community susceptible to invasion? Two commonly cited mechanisms are nutrient pulses and community diversity. In both of these, biological differences between native and invasive species can shift the community's competitive balance, especially when one group more effectively utilizes a nutrient pulse. These differences may play a role in invasions into a variety of habitats including deciduous forests and tallgrass prairie. As a biennial *Alliaria petiolata* (Garlic mustard, Brassicaceae) is active in deciduous forest understories during autumn and winter, allowing it to utilize nutrient pulses from leaf-litter before its competitors. I manipulated the timing of leaf-litter addition (fall or spring) and simulated the nutrient pulse from decaying leaves with artificial fertilizer addition. Fall nutrient-amended plots had greater adult biomass than plots receiving spring nutrient additions. In addition, silique production per plant and bolting stem was highest in fall litter-amended plots. Bienniality may provide a unique opportunity for *A. petiolata* to spread through deciduous forest understories.

Tallgrass prairie is dominated by high nutrient-use-efficiency warm-season (C_4) grasses and is frequently invaded by less nutrient-use-efficient cool-season (C_3) forbs. Physiological differences in phenology and nutrient-use efficiency may explain the invasion success of *Galium verum* (Rubiaceae), a European C_3 forb, in an experimental meadow at Blandy Experimental Farm. Within each of three warm-season grass diversity levels (one, three or five species), I performed four nutrient manipulations: 1) depleted nitrogen (excess carbon introduction), 2) ambient nitrogen, 3) elevated nitrogen (fertilizer

addition) and 4) fire (early-season burn). I found no effect of native grass diversity on the abundance of exotic *Galium*, nor did grass diversity significantly alter soil NO_3^- or NH_4^+ . Elevated nitrogen treatments produced significantly higher *Galium* biomass and stem density than depleted or ambient nitrogen treatments. The fire treatment significantly reduced *Galium* biomass relative to all other treatments. As predicted, soil plant-available nitrogen drove the pattern of *Galium* abundance, but early season fire inhibited *Galium* despite the nutrient release afterwards. Biological differences between exotics and natives in these systems may allow the invasive species to exploit nutrient pulses more effectively and expand their ranges.

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Chapter 1. Introduction

Importance of Invasive Species

Invasive species pose a serious threat to biodiversity worldwide. Species that, through human activities, occur outside their native range are known as exotics. Of those species, a number become established in their new habitat (Shea & Chesson 2002). These species may spread and in doing so cause the decline of native species (Mack et al. 2000, Mooney & Hobbs 2000). Invasive plants can drive the decline in native biodiversity in several ways. Invasives often out-compete native species for limiting resources, especially soil nutrients (e.g., Smith & Knapp 2001; Brewer & Cralle 2003; Gross et al. 2005). *Andropogon bladhii*, an invasive grass from Eurasia is better able to exploit low nutrient and water conditions than *Andropogon gerardii*, the most dominant species of the tallgrass prairie (Reed et al. 2005). *A. bladhii* drives soil resource levels below the minimum requirements for native species, driving them to extinction locally. *A. gerardii* typically dominates the tallgrass prairie due to its superior resource use efficiency, but is now threatened in some regions by a more efficient competitor. Invasive species also alter habitats; consequently natives can no longer survive (e.g., Lonsdale 1988; Wiedemann & Pickart 1999). The invasive tree *Acer platanoides* creates a very dense canopy, causing intense shading through which only *A. platanoides* seedlings can thrive. Reinhart et al. (2006) found that the understory of an *A. platanoides* forest receives <5% of the PAR of a native forest. Some invasive plants alter nutrient cycling through alteration of fire regimes, decomposition and litter production (e.g., Ehrenfeld 2003; Keeley et al. 2003; Rothstein et al. 2004). In Hawaii, the fire-adapted invasive grasses

Andropogon virginicus, *Schizachyrium condensatum* and *Melinis minutiflora* promote increased fire frequency by maintaining high dead:live biomass ratios, suppressing the slow-growing native plants and further altering the fire regime (Hughes et al. 1991).

Invasive species threaten half of the endangered species in the United States, especially plants and birds (Wilcove et al. 1998). Habitats invaded by exotic species typically show reductions in native biodiversity. This can have serious implications not just for the species being displaced, but also for species with which they have co-evolved (Toft et al. 2001). Declines in plant diversity have devastated the populations of insects that feed on and pollinate the plants.

Nutrient pulses and disturbance

Nutrient pulses, the “temporary availability of dramatically higher than normal levels of resources, which then become depleted with time” (Ostfeld and Keesing 2000), are responsible for many of the colonization and invasion events that occur worldwide. The link between disturbances and nutrient pulses has been studied extensively (e.g. Burke & Grime 1996; Vitousek et al. 1997). Not all disturbances introduce an excess of resources to a habitat, but oftentimes they create a net surplus of resources. This net increase in unsequestered resources can be brought about by two main mechanisms: a decrease in uptake of resources caused by the physical loss of biomass, or an increased absolute availability of resources sometimes released from dead biomass. Many invasive species have ruderal characteristics such as high growth rates under elevated nutrient conditions (Baker 1986), which allow them to exploit disturbances and subsequent resource pulses. In this framework, Davis et al. (2000) proposed the fluctuating resource

hypothesis to explain the establishment and spread of many invasive species. They stated that invasions most frequently occur after a disturbance due to an increase in resource availability. In the presence of suitable propagule density, these newly freed resources allow species to colonize a community. Often the colonizing species are native or benign exotic species, but pernicious invasive species can also become established.

The literature implicating excess nutrients in invasions is quite extensive (e.g., Brooks 2003, Siemann et al. 2007, Tyler et al. 2007). In many nutrient poor ecosystems, invasive species exist in low abundance (Leger et al. 2007). When these ecosystems are fertilized, invasive species often become more abundant. Brooks (2003) found that nitrogen fertilization increased the productivity and abundance of exotic annual species in the Mojave Desert. These increases in non-native species caused a decline in native plants, probably due to increased competition for nutrients. The conversion of coastal tallgrass prairie to *Sapium sebiferum* (Chinese tallow tree) monocultures was also facilitated by nitrogen fertilization (Siemann et al. 2007). In Willapa Bay, Washington *Spartina alterniflora* invasion into low nitrogen mudflats was limited by nitrogen concentration (Tyler et al. 2007). As further evidence of the competitive advantage of invasive species in high nutrient environments, the introduction of high carbon substrate (commonly sawdust or sucrose) to increase microbial nitrogen immobilization and deplete plant-available nitrogen has led to declines in invasive dominance in several grassland ecosystems (Alpert & Maron 2000; Corbin & D'Antonio 2004). These and many other studies highlight the significance of nutrient additions, especially nitrogen, in the worldwide expansion of invasive species. Current excesses of reactive nitrogen in the

environment caused by over-use of fertilizers and other practices (Galloway et al. 2004), will likely contribute to the continued spread of exotic species into new habitats (Stevens et al. 2004).

Not all nutrient pulses are anthropogenic. Disturbances are integral to the maintenance of many ecosystems (Sousa 1984). Following a disturbance, resources can be made available when nutrients are released from dead biomass. Habitats that feature natural, regular nutrient introductions are frequently referred to as pulsed communities (Ostfeld & Keesing 2000). In many forest ecosystems, leaf litter decay is an important source of nutrients that were previously unavailable to residents. The cycling of nutrients from leaf litter can have important implications for these systems. In long-term litter removal experiments, soil nutrients, especially in plant-available forms, are severely depleted (Wittich 1951). Another study found strong fluctuations in soil nutrients in areas from which litter had been removed (Mo et al. 2003). Litter removal also causes decreased tree growth, although it often takes several years for growth decline to manifest itself (Wiedemann 1935). Nutrient release from decomposing leaf litter may enhance seedling growth (Brearly et al. 2003) and also increase seedling survival (Sayer 2006). Leaf litter differentially affects seedling success, suppressing shade-intolerant species while having little effect on shade-tolerant seedlings (Sydes & Grime 1981). Although there is ample evidence of the importance of leaf litter in nutrient cycling and plant productivity (e.g., Sayer 2006), few studies have examined the effects of leaf litter on species invasions. The studies that have been performed focused mainly on the negative effects of leaf litter on germination and establishment (Meekins & McCarthy 2001;

Bartuszevige et al. 2007), yet nutrient pulses have important implications for the plant community. Increased resource abundance may alter the community dynamics and result in species invasions.

In many ecosystems fire is an integral component of the natural disturbance regime (Johnson et al. 2001; Keeley & Fotheringham 2001). Fire is an important disturbance because it releases nutrients sequestered in biomass that can be utilized by survivors or seedlings (D'Antonio & Vitousek 1992). Fire also provides an opportunity for germination in a less competitive environment, typically with higher light and nutrient levels (Turner et al. 1997). Many species have evolved tolerance to fire and some even require burning to germinate or reproduce (D'Antonio & Vitousek 1992). The nutrient pulses provided by fire benefit some invasive species (Chambers et al. 2007), but hinder others (Emery & Gross 2005; MacDonald et al. 2007).

Biodiversity and Invasibility

Biodiversity may be an important factor in community invasibility. Elton (1958) noted that oceanic islands, typically low in species diversity, supported high numbers of invasive species. Many researchers have expounded upon this concept over the past half-century (e.g., Tilman 1997; Dukes 2001; Kennedy et al. 2002). Proponents of a negative relationship between community diversity and invasive species abundance focus on the high niche space utilized by diverse communities (Naeem et al. 2000). The species that exist within a diverse community are able to utilize resources slightly differently due to niche separation among species, creating an environment in which a smaller portion of the resources are left unutilized. The dearth of unutilized resources from high diversity

communities is similar to the mechanism by which Davis et al. (2000) assert invasions are hindered in undisturbed communities. To successfully invade a community with low resource availability, the invading species' resource requirements (Tilman's R^*) must be lower than the R^* of the native species (Tilman 1982).

Observational data from larger scale studies (Levine & D'Antonio 1999) have provided support for a dissenting view: in order to support high diversity of native species, an ecosystem must possess the resources necessary to support high numbers of exotic species (Lonsdale 1999; Stohlgren et al. 1998, 1999, 2003). In other words, habitats that are good for native species are also good for exotic species. High ecosystem productivity is inherently destabilizing, resulting in frequent extinction and colonization events (May 1973). This instability may also increase the likelihood of exotic species establishment. Spatial heterogeneity may also explain the positive relationships seen on larger scales (Davies et al. 2005). At larger scales there are often a greater variety of niches available, promoting the coexistence of many species and creating a positive diversity-invasibility relationship.

Critics of the negative diversity-invasibility relationship championed by Tilman (Tilman 1997; Tilman et al. 1997) have cited statistical instead of ecological means by which more diverse communities both enhance productivity and decrease invasibility. Smith et al. (2004) found that the presence of a dominant species (*Andropogon gerardii*) had the greatest effect on community invasibility. A community dominated by one or a few species was better able to utilize available resources than several less dominant species. This study provided experimental evidence for the sampling effect: a dominant

species, in monoculture or in a diverse community, will have the greatest effect on invasibility (Crawley et al. 1999). This sampling effect, whereby more diverse communities contain by chance the most dominant species and thus have lower invasibility, is a statistical, not an ecological phenomenon (Aarssen 1997, Huston 1997, Tilman 1997). Thus, low diversity communities tend to lack the most dominant and resistant species through chance alone. Any correlation between diversity and invasibility is a statistical artifact. However when controlling for extrinsic factors by examining different spatial scales (i.e., neighborhood, community, landscape) separately a negative relationship between diversity and invasibility is found (Shea & Chesson 2002). In addition site productivity may alter diversity-invasibility relationships (Davies et al. 2007). More productive sites often feature greater competition, while less productive sites frequently promote species coexistence. We would expect to see positive relationships in low productivity sites and the reverse at high productivity.

Study Systems

This study examines two distinct systems that have been invaded by species whose life histories differ in important respects from the dominant native species. The understory of deciduous forests in Virginia is dominated by herbaceous perennial spring ephemeral species. These species typically grow and senesce before canopy closure occurs (Muller & Bormann 1976). The forest understory has been invaded by garlic mustard (*Alliaria petiolata* (M. Bieb) Cavara and Grande), a biennial herbaceous species. Garlic mustard has become the dominant species of this habitat through competition and allelopathic effects on natives (Meekins & McCarthy 1999; Roberts & Anderson 2001;

Callaway et al. 2008). In addition to these characteristics, garlic mustard's biennial habit may enhance its dominance. As a wintergreen species, garlic mustard is able to utilize nutrients made available through autumn and winter before its competitors become active. An important source of autumn nutrients may be decaying leaf litter. The ability of garlic mustard to utilize this natural nutrient pulse could help explain its success in North America.

In tallgrass prairie ecosystems, fire has been the most important large-scale disturbance (Collins & Steinauer 1998). Fire is also a common management tool. An important aspect of fire is the removal of standing litter and subsequent nutrient release from this biomass (Turner 1997). The dominant warm-season grasses often respond well to fire while woody species are harmed, allowing warm-season grasses to maintain their dominance in the face of shrub encroachment (Lett & Knapp 2005). However this nutrient pulse may facilitate invasion by herbaceous forbs. By removing biomass and releasing nutrients, fire creates a window in which species may colonize this habitat (Turner 1997).

In addition to these natural nutrient pulses, anthropogenic fertilization may have severe repercussions for many low-nutrient environments (Stevens et al. 2004). Cool-season species (C_3) typically exhibit higher growth rates when exposed to large nutrient supplies than warm-season species (C_4) (Chapin 1980). This physiological difference may explain the invasion of the C_3 forb *Galium verum* into the warm-season grass meadow at Blandy Experimental Farm. *Galium*, an herbaceous perennial forb, is the most abundant exotic species in the meadow. *Galium* may use both natural (fire-mediated) and

anthropogenic nutrient pulses to gain an advantage over the more nutrient-use efficient warm-season grasses.

Objectives

Invasive species can severely alter ecosystem function and decrease biodiversity. Once an invasive becomes established, it is often prohibitively expensive to restore the ecosystem. In severe cases, ecosystems can be permanently altered by invasive species. It is important to understand the mechanisms by which exotic species enter communities. High invasibility might be an intrinsic characteristic of communities, however certain events, such as disturbances might also facilitate invasions. Increased human-induced alterations to disturbance regimes necessitate our understanding of the dynamics involved in disturbance-facilitated invasion. If we understand the circumstances under which colonization occurs, we will have greater power to predict habitat vulnerability to invasion. This study examined two questions that have been proposed in either facilitating or inhibiting the invasion of plants into native communities:

- 1) Do nutrient inputs facilitate the invasion of communities by exotic species?
- 2) Does community biodiversity affect invasibility?

Chapter 2. The utilization of leaf-litter nutrient pulses by *Alliaria petiolata*, an exotic wintergreen species.

Introduction

In many systems, invasion is facilitated by disturbances (e.g., Hobbs & Atkins 1988; Burke & Grime 1996; Vitousek et al. 1997). These events decrease competition in the community and often increase resource availability. Davis et al. (2000) proposed the fluctuating resource hypothesis to explain increases in invasibility with disturbance. The theory suggests that invasions occur when the utilization of a limiting resource declines, usually through disturbance, or the supply of the resource is increased. In an undisturbed system, the resident community utilizes nearly all of the resources. These residents typically use nutrients to the extent that invading propagules cannot establish (Davis & Pelsor 2001). This study, however, will examine an invasive species with a life-history which may allow it to intercept nutrients before they become available to the native community.

Many invasive plants are ruderals (Baker 1986), which thrive on disturbance and grow quickly under high nutrient conditions (Grime 1979). Invasive plants are often found at forest edges and in riparian zones, where water and light are abundant (Brothers & Spingarn 1992; Stohlgren 1998; Nuzzo 1999). Although light and water are essential resources, nutrient pulses have also been shown to facilitate invasions (Morghan & Rice 2006; Olson & Blicher 2003). In Mediterranean nutrient-poor ecosystems of western Australia, increased fire frequency has elevated soil phosphorus levels and, subsequently,

invasion of woodlands by exotic grasses (Fisher et al. 2006). The fertilization of native-dominated serpentine grasslands in California quickly caused a shift in composition toward invasive species (Huenneke et al. 1990; Thomsen et al. 2006). Anthropogenic modification has altered disturbance regimes and increased nutrient inputs to many naturally nutrient-poor habitats, frequently facilitating plant invasions (Vitousek et al. 1997; Lowe et al. 2003).

Many nutrient-facilitated invasions are the result of anthropogenic eutrophication (Vitousek et al. 1997), but natural nutrient pulses are also crucial for some invasions (Hobbs & Mooney 1991; D'Antonio & Vitousek 1992). Although not all invasions are mediated by nutrient additions, the timing of natural nutrient release may be an important determinant of community susceptibility to exotic species invasion. In temperate ecosystems nutrient uptake varies seasonally, with little use of resources during winter. Nutrients released during this dormant period may remain unutilized for some time. A species that is able to utilize a resource while its competitors are dormant could gain an advantage over these species and become more dominant. Nutrient release and uptake are not always coupled temporally (Muller & Bormann 1976; Anderson & Eickmeier 2000), allowing species possessing novel traits to exploit the pulse and dominate naïve communities. Exotic species possessing unique traits could establish and spread without the aid of disturbance or eutrophication.

Garlic mustard (*Alliaria petiolata* (M. Bieb) Cavara and Grande), an important invader of deciduous forests throughout eastern North America (Welk et al. 2002), now inhabits many areas with a history of anthropogenic disturbance. These disturbances may

have facilitated its initial invasion. Biennial species, including *A. petiolata*, are most prevalent in habitats disturbed every one to three years (Viswanathan & Aarssen 2000). As a biennial, *A. petiolata* is wintergreen (Cavers et al. 1979), which may give it an advantage throughout its North American range. Although it is not very active during the winter, some growth does occur during warmer periods. Growth while the majority of its perennial competitors are completely dormant may give *A. petiolata* a competitive advantage. Under an open canopy, *A. petiolata* receives relatively high irradiance during the winter months. Winter photosynthesis, even in small amounts, can help *A. petiolata* bolt early in spring. Bolting plants sometimes elongate by as much as 1.9 cm/day (Anderson et al. 1996). Carbon and nutrients stored during winter should facilitate this rapid growth.

Because most of the understory is composed of spring ephemeral species that are dormant through the winter, the wintergreen *A. petiolata* may gain nutrients from the decomposition of autumn leaf litter before its competitors can access them. Litter decomposition acts as an unsequestered nutrient pulse (Anderson & Eickmeier 2000; Park & Matzner 2003) that may give *A. petiolata* an advantage over native spring ephemerals. The wintergreen habit may be garlic mustard's "triggering attribute," a trait that is uncommon in the invaded range and allows an exotic species, once established, to dominate the system (Gurvich et al. 2005). In this study I sought to answer two questions:

- 1) Does early nutrient availability allow *A. petiolata* to reach greater size and fecundity?

2) Does fall nutrient availability increase *A. petiolata*'s advantage over spring ephemeral species, allowing it to outcompete native species and decrease biodiversity?

Methods

Alliaria petiolata

Alliaria petiolata (M. Bieb) Cavara and Grande is an invasive understory plant of the mustard family (Brassicaceae) native to Eurasian temperate forests (Bossdorf et al. 2004a). *A. petiolata* is an obligate biennial in North America, but may be a winter annual or biennial through its native range (Dhillion & Anderson 1999). It was first recorded in North America in 1868 on Long Island, New York (Nuzzo, 1993), however garlic mustard has since been introduced into North America several more times (Durka et al. 2005). Seedlings germinate in the early spring and form a non-reproductive rosette consisting of several small leaves. The plant overwinters as a rosette, growing slowly until mid-spring when each individual shoot produces numerous small flowers each containing several siliques (Cavers et al. 1979). Smith et al. (2003) found each silique to contain on average 7.8 seeds.

A. petiolata combines traits of native understory species, such as shade tolerance and large seeds, with characteristics that promote dominance for introduced plants, such as a lack of parasites and herbivores (Cruden et al. 1996). Allelopathy may also give garlic mustard an advantage over native species (Roberts & Anderson 2001). These traits, along with large seed pools, allow garlic mustard to be a very successful invader. This

species exhibits some phenotypic plasticity in response to variation in habitat, which tends to increase fitness. Dhillon and Anderson (1999) found that individuals grown in forests displayed their highest photosynthetic rates and stomatal conductance at medium irradiance, while high light corresponded with lower assimilation. Although *A. petiolata* can reproduce sexually, its self-compatibility allows a single individual to establish a population (Davis et al. 2006). Seeds can remain dormant in the seedbank for five years (Baskin & Baskin 1992) posing a problem for control measures. This long dormancy period can allow *A. petiolata* to quickly exploit disturbances. Garlic mustard thrives on disturbance, often being found along forest edges and flood plains (Nuzzo 1999; Meekins & McCarthy 2000; Stinson et al. 2006).

A. petiolata is distributed throughout suitable habitat in the northeastern United States, ranging south to North Carolina and west to Illinois (Welk et al. 2002). The species will presumably continue to spread from its current range, establishing preferentially in disturbed habitats (Stinson et al. 2006). It is able to invade forests with intact litter layers, but prefers mesic open-canopied forests (Meekins & McCarthy 2001). Others have noted garlic mustard's ability to invade second-growth forests, habitats that resist invasion relatively well (McCarthy 1997). Nuzzo (1999) approximated *A. petiolata*'s rate of spread through high quality habitat and believed this rate to underestimate the actual migration rate due to the prevalence of highly disturbed forests. Within its native range, garlic mustard benefits from anthropogenic disturbances and is becoming more prevalent across Eurasia (Welk et al. 2002).

Study Site

The 17-hectare, second growth woodlot at Blandy Experimental Farm in Boyce, VA (39°5' N, 78°3' W) contains a moderate infestation of *A. petiolata*. Mean annual precipitation at Blandy is 940 mm/year. This 100-year old forest has a canopy dominated by deciduous species, mainly *Carya tomentosa*, *Celtis occidentalis*, *Quercus alba*, *Quercus rubra*, *Nyssa sylvatica*, *Prunus serotina* and *Liriodendron tulipifera*. The shrub layer consists predominantly of *Cornus florida*, *Asimina triloba*, *Viburnum prunifolium*, *Sassafras albidum* and *Lindera benzoin*. Several exotic species, including *Lonicera maackii* and *Ligustrum* spp., are also abundant. The understory is composed mainly of perennial spring ephemeral species that perform most of their growth and reproduction between snowmelt and canopy closure (Rothstein 2000). The effects of shading from *A. petiolata* during this time of otherwise high light on the forest floor could have dramatic effects on spring ephemerals. Ephemeral species are important because their growth occurs in early spring, the period of greatest nutrient loss from ecosystems (Muller & Bormann 1976). During this time, these species may sequester nutrients that would otherwise be lost from the system.

Nutrient Manipulations

The experiment included six treatments (Table 1). Two of these treatments (Treatments 1 and 3) represented autumn nutrient inputs through either leaves or artificial fertilizer (Osmocote). Two treatments (Treatments 4 and 5) represented spring nutrient inputs as leaf litter or fertilizer. One treatment (Treatment 2) received no nutrient inputs and another treatment (Treatment 6) received autumn leaf litter, but all garlic mustard

rosettes were removed. Treatment 6 was included only in the analyses of the effects of garlic mustard and nutrient treatments on other members of the herbaceous community.

Table 1. Garlic Mustard Treatment Manipulations

Treatment 1	Remove Nothing	Leaves collected in screen spread evenly over plot
Treatment 2	Remove Litter	Leaves collected and discarded. Ground free of debris.
Treatment 3	Remove Litter, Fall Fertilizer	Leaves discarded. Ground cleared, fall artificial nutrient.
Treatment 4	Remove Litter, Spring Fertilizer	Leaves discarded. Ground cleared, spring artificial nutrients
Treatment 5	Add Leaves in Spring	Leaves collected in autumn, reapplied to plot in spring.
Treatment 6	Remove Garlic Mustard	Garlic mustard removed. Leaves collected, spread on plot.

Fifteen replicates of these six treatments were established at Blandy on October 22, 2006. Each plot measured 0.46 m². A 15 cm high barrier, created using landscaping fabric (Greenscapes General Purpose Landscape Fabric), surrounded each plot to prevent leaves and other debris from blowing onto the plot. Each plot was covered by a mesh net 60 cm above the ground in order to catch falling leaves. Nets were cleared frequently to prevent shading and leaching of nutrients from debris during rainfall.

Forest floor leaf litter was left undisturbed in Treatment 1 and litter caught above these plots was distributed evenly across the plot. Supplemental litter was added to some plots to match the leaf litter depth immediately outside the plot.

Replicates of treatments 2, 3, 4 and 5 were cleared of leaf litter in October 2006, as these treatments did not receive autumn leaf litter. All plots from these treatments (2, 3, 4 and 5) were checked periodically and cleared of litter until leaf senescence ceased in late November. Each of these treatments received artificial leaves in November 2006 to mimic physical properties of litter. These characteristics include insulation, moisture

retention and shading. To make these “leaves” I cut landscaping tarp^[dci1] (Greenscapes General Purpose Landscape Fabric) into small leaf-size pieces (~ 8 x 8 cm squares). Treatment 2 (T2) was maintained without leaf litter or nutrient addition. In Treatments 3 and 4, artificial fertilizer was utilized to mimic the natural loss of nutrients from leaf litter decomposition and leaching. Cromack and Monk (1974) found that a mixed deciduous forest releases 0.283 g N/m²/year to the soil from leaf litter. 0.991 g Osmocote, a slow-release fertilizer, was added to Treatments 3 and 4 (autumn and spring artificial nutrients, respectively). The slow release of nutrients from Osmocote more closely mimics the natural decomposition and release of nutrients from leaf litter. Artificial nutrients (Osmocote fertilizer) were added to Treatments 3 and 4 to determine whether nutrients released from decomposing leaf litter affected garlic mustard growth and reproduction.

Leaf litter was collected from Treatment 5 (T5) and stored overwinter. To test whether spring nutrient pulses are utilized by and also benefit *A. petiolata*'s competitors, leaf litter was reapplied to these plots on March 24, 2007. In treatments 3 and 4 (T3, T4), Osmocote fertilizer was added as prescribed above. T3 received fertilizer on November 19 to mimic autumn leaf litter (T1). T4 received fertilizer on March 24 to mimic spring leaf-litter addition (T5). To assess the effect of *A. petiolata*'s presence on its competitors, all *A. petiolata* plants were removed from Treatment 6 (T6) on November 19. Similar to T1, leaves captured on T6 were also redistributed within the plot.

Initial Measurements

The number of leaves per plant was counted on October 28 and 29, prior to any manipulations. These served as base measurements from which to compare individuals

after manipulations. The number of plants per plot was also surveyed prior to manipulation.

Adult Growth and Reproduction

On April 29, the number of bolting stems per plot was counted. All plants were harvested in June 2007 following silique production. Plants were separated into aboveground, belowground and reproductive biomass. Aboveground biomass was oven dried and weighed. Plants per plot, stems per plant, stems per plot, and aboveground biomass per plot, plant and stem were calculated. Siliques were harvested from adult plants and the number of siliques per stem, siliques per plant and siliques per plot were counted.

Competitor Diversity

The impact of *A. petiolata* on native herbaceous species was also determined. Individuals of other understory species were identified and counted in all plots. Plot diversity was calculated using the Shannon-Weiner and Simpson Diversity Indices. Community diversity was also measured using species richness, the total number of species present within a plot, and species evenness. The number of individuals of all species other than *A. petiolata* in each plot was also counted.

Statistical Analyses

All data were tested for normality and homogeneity of variances. Transformations were performed when necessary to meet assumptions. Repeated measures ANOVAs using Proc Mixed in SAS (SAS Institute Inc., Cary, NC, Version 9.1) were performed on plant number in October and June with nutrient treatment and time as fixed effects and

block as a random effect. Repeated measures ANOVA were also performed on bolting stems per plot between April and June.

Autumn plant density (October, 2007) differed significantly among treatments ($p = 0.031$), although there were no treatments that had significantly different mean density when all pairwise comparisons were performed with Ryan's Q. Nonetheless initial density was retained as a covariate for subsequent analyses. ANCOVAs with October plant density as a covariate were performed only on plot aboveground biomass and siliques per plot, as these were the only response variables for which the covariate effect had significant explanatory value and all ANCOVA assumptions were satisfied (i.e., non-significant initial density*treatment interaction). ANCOVAs were performed in SAS 9.1 PROC GLM with treatment as a fixed effect, block as a random effect, and October garlic mustard density as a covariate.

Two-way ANOVA in SAS 9.1 using a general linear model with block as a random effect and nutrient treatment as a fixed effect were performed on plants per plot, stems per plot, stems per plant, siliques per plant and siliques per stem. Two-way ANOVAs were also performed on all competitor diversity and richness indices.

Planned contrasts were performed for all response variables that produced a significant treatment effect. The following contrasts were used: Fall leaf litter vs. Spring leaf litter; Fall artificial nutrients vs. Spring artificial nutrients; Fall nutrients (leaves or artificial nutrients) vs. no nutrients; Spring nutrients vs. no nutrients; Fall nutrients vs. Spring nutrients. Experiment-wise error rates were maintained with the Dunn-Sidak adjustment (5 contrasts, $\alpha' = 0.01021$). A sixth contrast was also performed for

competitor analyses: garlic mustard removal vs. all garlic mustard plots. Thus the adjusted α' for all competitor contrasts (6 contrasts) was 0.00851. When no contrasts showed significant differences among groups for a given response variable, all pairwise comparisons were performed using the Ryan's Q test. When there were unequal sample sizes, I used the Tukey-Kramer test instead of Ryan's Q.

Results

Above-ground Biomass

There was a highly significant difference among treatments in total *A. petiolata* aboveground biomass at senescence in June 2007 (Table 2a) with initial garlic mustard density as a covariate. Treatments receiving fall leaves had significantly greater above-ground biomass than fall artificial nutrient treatments (Figure 1).

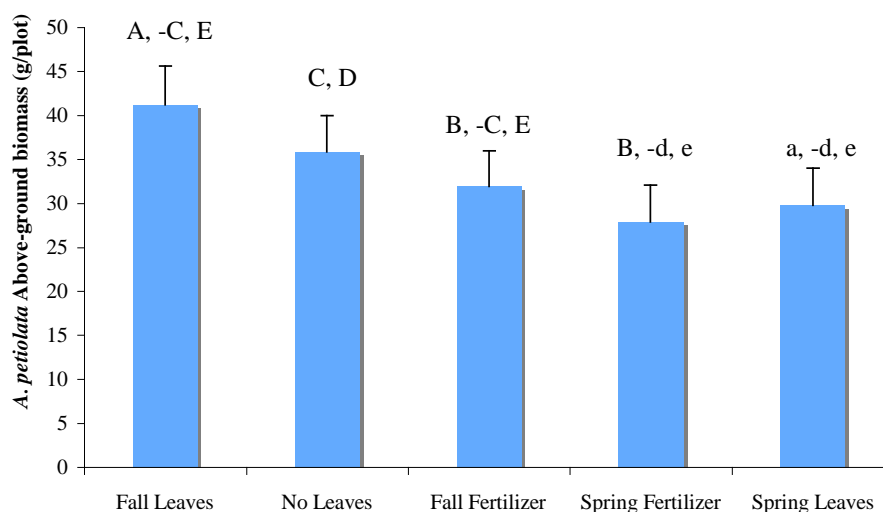


Figure 1. Aboveground biomass of *A. petiolata* (mean + 95% CL) harvested after seed maturation in June 2007. Similar letters indicate contrasts. A capital and lowercase letter indicate a

significant difference between treatments. Two (-) letters indicate treatments combined for a given comparison. All comparisons were performed with α adjusted using the Dunn-Sidak method. Plants that received fall nutrients (either leaf litter or artificial nutrients) produced significantly greater above-ground biomass than plots that received either nutrient type during spring. Surprisingly, spring nutrient additions (as fertilizer or leaf litter) produced significantly less plot biomass than plants that never received nutrients (T2). Total plant density (Figure 2) was not significantly different among treatments (Table 3a) when plots were harvested in June.

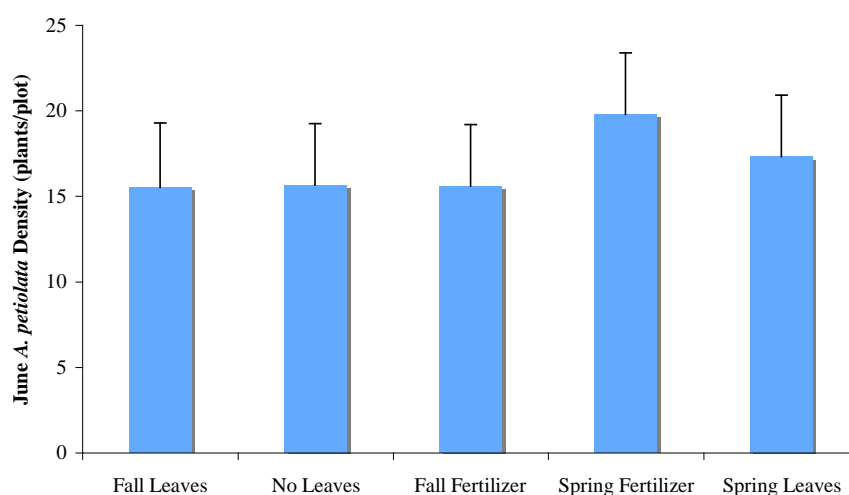


Figure 2. The density of bolting adult *A. petiolata* plants (mean + 95% CL) at seed maturation in late June 2007. Differences among treatments were not significant ($p = 0.39$).

Bolting Stems

Based on repeated-measures ANOVA, there was a significant effect of time on bolting stem number, but the interaction between nutrient manipulation and time was not significant (Table 4). In other words the number of bolting stems increased between April and June, but the increase was similar across all treatments. The number of bolting stems per plot did not differ significantly among treatments in June 2007, nor were there

significant differences among treatments in April bolting stem density indicating that additional nutrients accumulated by individuals were not utilized to grow additional stems (Figure 3).

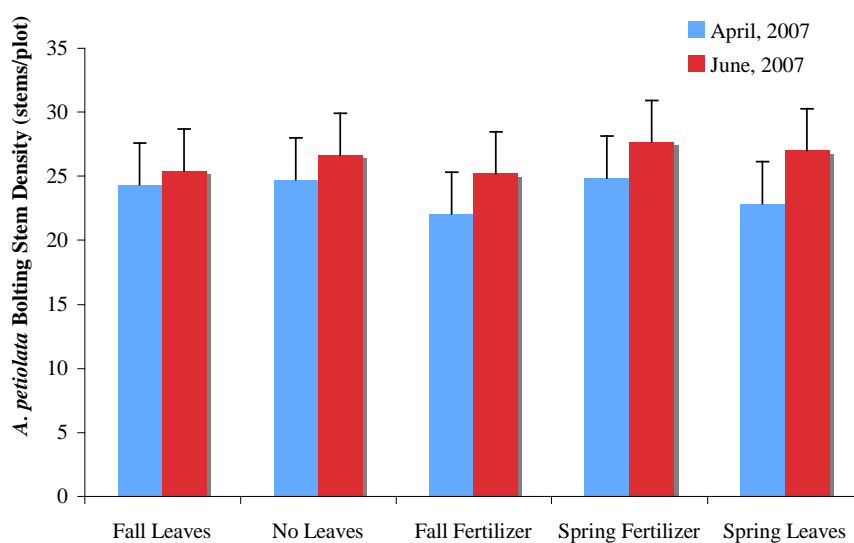


Figure 3. The number of bolting stems of *A. petiolata* per plot in April (blue) and June (red), 2007. Plants began to bolt in April and senesced in June. There was no effect of treatment on stem number on either date (April $p = 0.79$; June $p = 0.96$).

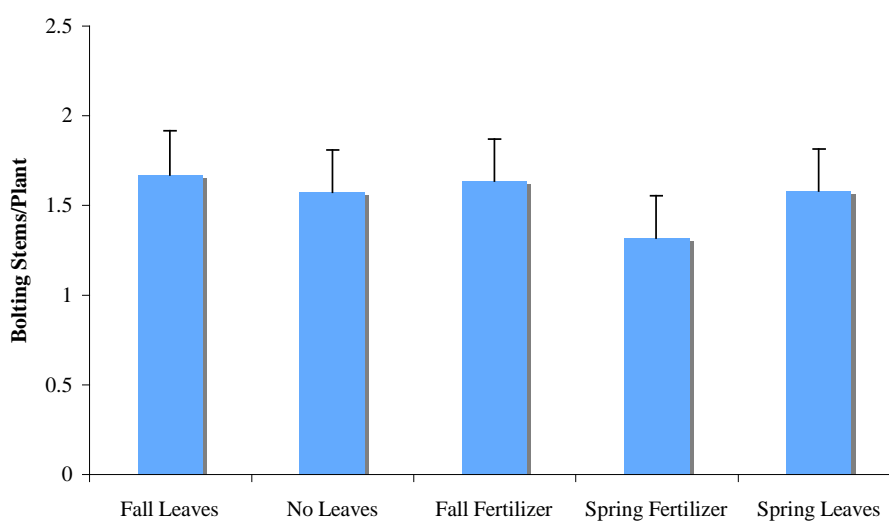


Figure 4. The number of bolting stems of *A. petiolata* per plant (mean + 95% CL) within a plot.

Stem production within plants did not vary among treatments ($p = 0.26$).

There was also no significant effect of nutrient manipulation on the number of bolting stems per plant (Table 3b). Individual plants did not allocate additional nutrients to increased stem growth (Figure 4).

Reproductive output

Based on ANCOVA there was a significant treatment effect on silique production per plot (Table 2b), however none of the planned contrasts showed significant differences among groups (Figure 5). Plots receiving autumn leaf litter had the largest reproductive output, a mean of 510.4 (+/- 37.8) siliques, while spring artificial nutrient addition plots produced the fewest siliques (328.1 +/- 37.12).

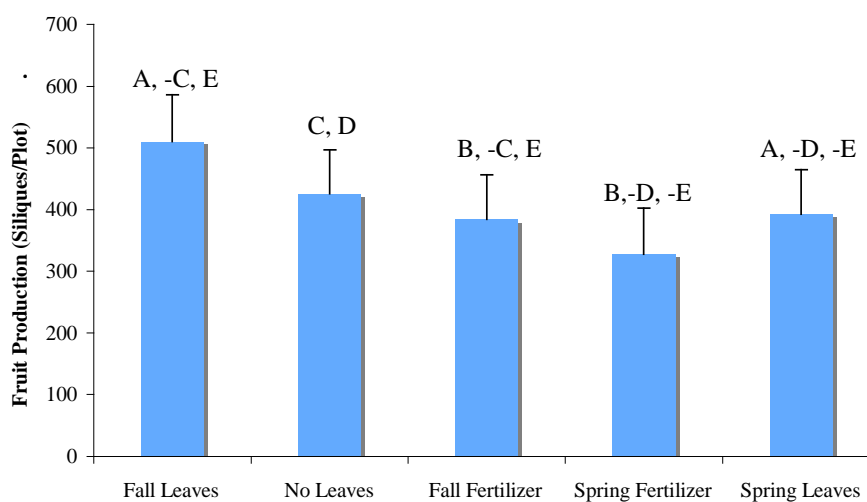


Figure 5. The number of *A. petiolata* siliques produced within a plot in June 2007 (mean + 95% CL). Although the overall ANCOVA showed a significant treatment effect, no contrasts produced significant differences among treatments. Shared letters denote planned comparisons. All comparisons were performed with α adjusted using the Dunn-Sidak method ($\alpha' = 0.1274$).

There was also a significant effect of nutrient addition on reproduction per bolting stem (Table 3c). Fall leaf litter addition yielded significantly greater silique production per bolting stem (17.76-silques/stem) than either artificial nutrient treatment (Fall or Spring). Fall artificial nutrient addition plots produced 13.64-silques/stem, while plots receiving spring artificial nutrients averaged 13.31-silques/stem. Both spring leaf-litter and no nutrient addition produced similar numbers of fruits per stem (Figure 6). Plots receiving fall leaf litter produced significantly more siliques per individual than the spring fertilized plots (30.45 and 17.50 siliques/plant respectively) (Table 3d). Spring leaf litter, fall artificial nutrients and no nutrient addition plots had approximately equal production of siliques per individual (Figure 7).

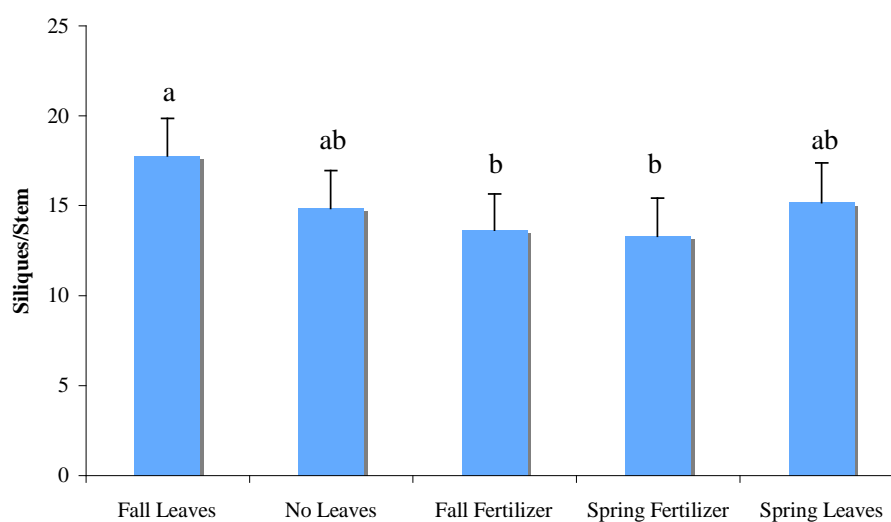


Figure 6. Silique production per bolting stem in *A. petiolata* (mean + 95% CL) harvested in June 2007. Plots receiving Fall leaf litter had significantly greater silique output per bolting stem than either fertilizer treatment.

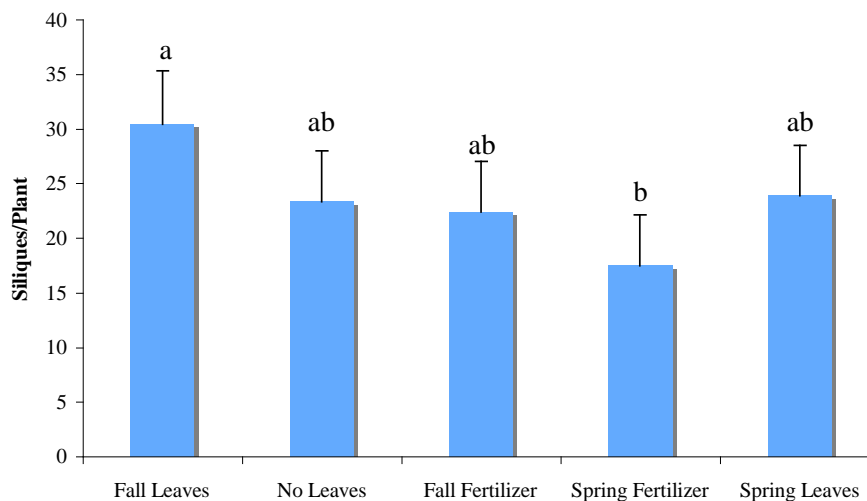


Figure 7. Silique output per plant (mean + 95% CL) from June 2007. Fall leaf litter enabled individuals to produce a greater number of siliques than plots fertilized in Spring. No other differences were significant at $p = 0.05$. Shared letters denote no significant difference at $\alpha = 0.05$. Pairwise comparisons were performed using the Tukey-Kramer method.

Competitor Analysis

No effect of *A. petiolata* treatment on competitor diversity (all species excluding *A. petiolata*) was detected in this study. Based on individual species counts, there were no differences among treatments in competitor diversity using either the Shannon Diversity Index (Table 3e) or the Simpson Diversity Index (Table 3f). *A. petiolata* removal plots had slightly lower diversity values than any treatment containing *A. petiolata* according to either index (Figure 8a, b). Species evenness, another measure of species diversity, (Figure 8c) was not significantly affected by *A. petiolata* treatment (Table 3g). Likewise, there was no significant effect of *A. petiolata* treatment on species richness (Table 3h)

(Figure 8d). Despite *A. petiolata*'s dominance in the understory, I found no effect of *A. petiolata* on the diversity of its competitors.

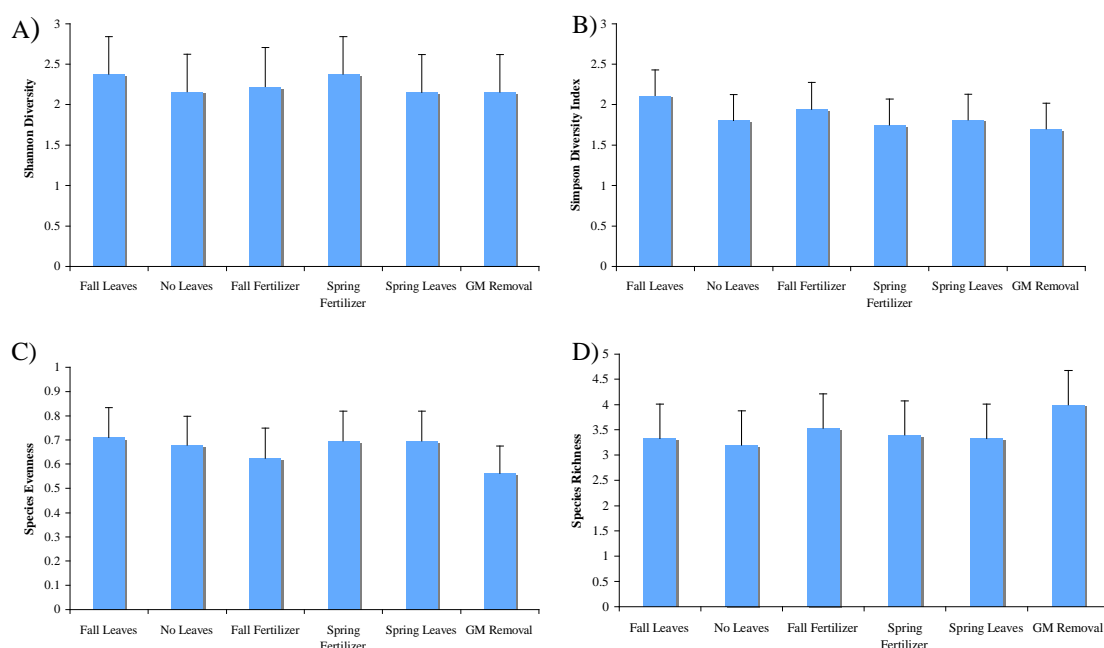


Figure 8. **A)** Community diversity calculated with the Shannon Diversity Index. Shannon diversity did not vary significantly among groups ($p = 0.95$). **B)** Community diversity calculated with the Simpson Diversity Index. Simpson diversity was not significantly affected by treatment ($p = 0.50$). **C)** Community evenness of *A. petiolata*'s competitors within experimental plots. There were no significant differences in species evenness among treatments ($p = 0.45$). **D)** Species richness (total species present) in experimental plots. There was no significant effect of *A. petiolata* treatment on species richness ($p = 0.63$). Error bars represent mean + 95% CL.

Unlike diversity, competitor stem density (Figure 9) was significantly affected by *A. petiolata* treatment (Table 3i). Plots from which *A. petiolata* was removed contained a significantly greater number of stems than those plots receiving spring leaf-litter. Plots from which garlic mustard was removed contained a mean of 45.97 competitors. A mean of 24.70 competitor stems occurred in the spring leaf litter treatment. There were no differences among any other treatments.

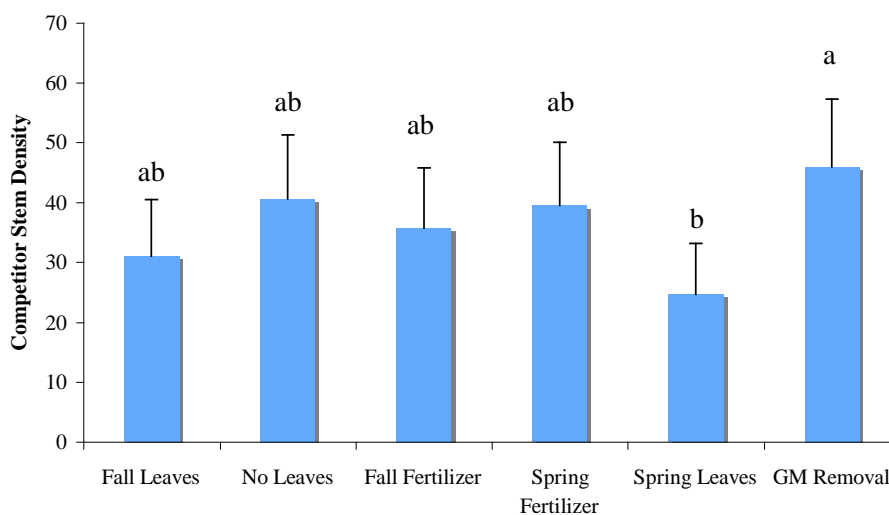


Figure 9. The total number of stems of *A. petiolata*'s competitors (mean + 95% CL). Shared letters denote no significant difference at $p = 0.05$.

Discussion

Garlic mustard growth and reproduction

I found some support for the hypothesis that autumn leaf litter acts as a nutrient pulse that could facilitate garlic mustard invasion. In this study, garlic mustard responded to fall nutrient additions (either leaves or fertilizer) with greater biomass production than when receiving spring nutrients. Fall leaf litter nutrient release also promoted increases in adult size over plants that received spring leaves. Plots that received no nutrients had greater above-ground biomass than those that received spring nutrient pulses. These results indicate that early acquisition of nutrients provides the greatest benefit to garlic mustard. In fact, late acquisition of nutrients appears to inhibit biomass production, although this result may be due to competition with other species for nutrients during

spring. Leger et al. (2007) found that native species in fertilized plots performed worse than native species in unfertilized plots through a combination of competition with invasive species and increased herbivory on more palatable (higher tissue N) plants. Although leaf_[dec2] litter nutrients did not have a strong effect on all aspects of garlic mustard's life history, there were some important increases in fecundity and survival that can be ascribed to autumn leaf litter addition.

Variation among treatments in the initial density of *A. petiolata* rosettes may have obscured some differences among treatments in final abundance and reproductive measures in my experimental plots. By chance, the plots to which the spring artificial nutrient addition treatment was applied were more densely populated with garlic mustard than other treatments. I used initial density as a covariate in the analyses, but treatment effects could have been obscured if density effects were nonlinear – especially if very high densities begin to suppress individual growth. In an experiment similar to this one, individual plants showed suppressed biomass and reproduction under extreme high density/high nutrient conditions (Meekins & McCarthy 2000). Individual plants in that experiment grown at lower density exhibited a substantial increase in biomass and reproductive output upon receipt of the same nutrients. Similarly, experimentally thinned populations had significantly greater biomass and reproductive output per individual (Rebek & O'Neil 2006). Densities in the Meekins & McCarthy (2001) and Rebek & O'Neil (2006) studies were 2-3 times the typical density in my plots, however, so it may be unlikely that the suppressive effects of extremely high density influenced the outcome.

Several measures of reproductive output exhibited substantial benefits from fall nutrient inputs through leaf litter. Silique production by individual plants and individual stems was significantly greater in plants receiving autumn leaf litter than spring artificial nutrient-amended plants. The autumn leaf litter treatment also produced more siliques per bolting stem than spring and fall artificial nutrient addition. Fall leaf litter may have provided benefits that artificial leaf litter could not replicate.^[doi3]

Davis et al. (2006) found annual fecundity to be an important demographic rate. Populations that produced fewer seeds spread less rapidly and were more easily controlled than more fecund populations. Increases in total silique production per area may have the greatest effect on rate of spread and degree of dominance of *A. petiolata* in a community (Davis et al. 2006). Higher silique production per individual plant or stem would be important in sparse satellite populations by shortening the time from initial establishment of *A. petiolata* to dominance in the community.

Effects on other species

The presence of garlic mustard reduced the stem density of other competing species within the plot. Carlson and Gorchoff (2005) found that areas from which garlic mustard was removed with herbicide had higher cover of natives, specifically spring ephemeral species. In my study, plots given leaves during spring had the lowest density of other (non-garlic mustard) species. Spring ephemeral species in this treatment may not have received nutrients quickly enough to increase their density. Spring ephemerals grow and reproduce before canopy closure (Muller & Bormann 1976), leaving only a small window through which nutrients may benefit the species. Since there were no significant

effects of the spring leaf treatment on garlic mustard size or fecundity, these leaves could have directly inhibited competitor species by decreasing light to the forest floor.

Seedlings would have been unable to germinate and reemerging individuals may not have been able to grow through the leaf litter quickly enough to maximize photosynthesis and growth.

The greater biomass and increased individual reproductive output afforded by early nutrient acquisition by *A. petiolata* may eventually it to exert a stronger influence on resident species. Although *A. petiolata* significantly reduced the number of resident species stems, its negative effects were not altered by any of the nutrient treatments. It is unclear whether increased individual fecundity will manifest itself with increased density of garlic mustard in the future. If the enhanced fecundity of garlic mustard accompanying the fall nutrient inputs from leaf litter results in higher recruitment, the greater density of *A. petiolata* will likely increase its influence on competitor species in coming years.

I found no effect of garlic mustard on the diversity of competitor understory species using species evenness, species richness, the Simpson Diversity Index, or the Shannon Diversity Index. Other studies have produced similar results: after five years of garlic mustard removal, Hochstedler et al. (2007) still found no increases in native species richness or diversity. This however, runs contrary to Meekins and McCarthy (1999), who found that garlic mustard was a superior competitor to *Quercus prinus* and may aggressively invade suitable habitat and displace *Q. prinus*. Garlic mustard is well established at Blandy and has persisted for several years. It is likely that whatever declines in species diversity that could be attributable to *A. petiolata* have already

occurred. The removal of individuals from a small area (0.46m^2) would not have opened up enough space for the spread of species most affected by garlic mustard's dominance.

Conclusions

Nutrient pulses may not explain invasions in all systems (e.g., LeJeune et al. 2006). Increased resource levels can provide an advantage to native communities being invaded by species that more efficiently utilize limiting resources. *Imperata cylindrica*, an exotic grass with lower nutrient requirements than longleaf pine, declined in abundance when phosphorus was added to longleaf pine savannas in the southeastern United States (Brewer & Cralle 2003). In New Zealand short tussock grasslands, periodic nutrient pulses did not increase the success of an invasive forb (Walker et al. 2005). The invasive *Andropogon bladhii* can more efficiently use resources than native *Andropogon gerardii* in low nutrient environments like the North American tall grass prairie (Reed et al. 2005). Resource pulses do not facilitate all invasions, but many systems, including the eastern deciduous forest, appear to succumb to invasive species when these exotics are able to utilize unsequestered resources.

My results provide support to the fluctuating resource hypothesis (Davis et al. 2000). *A. petiolata* appears to exploit unutilized dormant-season nutrient pulses to increase growth and reproduction. These nutrient pulses may have facilitated *A. petiolata* establishment in North America. The wintergreen nature of garlic mustard provides the species with the opportunity to grow and sequester nutrients while the majority of its competitors are dormant. Nutrients received during the spring appear to provide little benefit in the form of increased adult biomass or fecundity, while fall leaves allowed

garlic mustard to produce the greatest adult biomass. The ability to emerge early in the growing season can yield considerable fitness gains (Jones et al. 1997). As a wintergreen biennial, garlic mustard is able to capitalize on nutrients made available during autumn and the beneficial conditions early in the growing season. Wintergreenness may be the triggering attribute that allows garlic mustard, once present to expand within the forest understory. Since there are few invasive biennials, it is important to more fully understand the implications that this uncommon life-history has for the future spread of the species.

Table 2. Results of Analysis of Covariance. A) Adult *A. petiolata* above-ground biomass, B) Silique production per plot. *** denotes significant effect at $p = 0.05$. October juvenile rosette density was used as a covariate.

	A) Biomass			B) Siliques		
	df	MS	F	df	MS	F
Treatment	4	327.35	*** 5.67	4	53010.43	*** 3.06
Covariate	1	1197.26	*** 20.72	1	503459.35	***29.05
Block	14	448.08	7.76	13	107606.88	6.21
Error	51	57.78	--	50	17329.22	--

Table 3. Results of Analysis of Variance. A) Adult plants per plot at senescence in June, B) Number of bolting stems per adult plant, C) Silique production per bolting stem, D), Silique production per adult plant, E) Shannon Diversity index for competitor species, F) Simpson Diversity index for competitor species, G) Total competitor species richness, H) Total number of individuals of all competitor species within a plot, I) Species evenness of competitor species. *** denotes significant treatment effect at $p = 0.05$.

	A) Adult Plant Density			B) Stems/Plant		
	df	MS	F	df	MS	F
Treatment	1	50.42	1.05	4	0.28	1.38
Block	14	158.26	3.29	14	0.57	2.78
Error	54	48.12	--	54	0.20	--
	C) Siliques/ Stem			D) Siliques/ Plant		
Treatment	4	42.85	*** 2.86	4	304.72	*** 3.77
Block	14	69.11	4.62	14	351.95	4.36
Error	51	14.96	--	54	80.81	--
	E) Shannon Diversity Index			F) Simpson Diversity Index		
Treatment	5	0.18	0.22	5	0.34	0.89
Block	14	1.62	2.00	14	1.01	2.63
Error	69	0.81	--	69	0.38	--
	G) Species Evenness			H) Species Richness		
Treatment	5	0.05	0.95	5	1.20	0.70
Block	14	0.11	2.21	14	9.15	5.32
Error	61	0.05	--	70	1.72	--
	I) Competitor Density					
Treatment	5	6.22	*** 2.64			
Block	14	41.39	17.59			
Error	70	2.35	--			

Table 4. Results of Repeated-measures analysis of variance. Bolting stem density per plot counted soon after bolting initiated (April) and June when adult plants set seed and senesce.

Source	Bolting Stems		
	df	F	p
Treatment	4	0.41	0.8
Time	1	4.3	0.04
Treatment*Time	4	0.35	0.84
Error	121	--	--

Chapter 3. Disturbance not community diversity affects the success of exotic *Galium verum* in a Virginia grassland.

Introduction

Since Elton (1958) noted that oceanic islands, typically low in species diversity, supported higher numbers of invasive species, biodiversity has been considered an important factor in community invasibility. Over the next half century this idea has gained much support (e.g., Tilman 1997; Naeem et al. 2000; Hector et al. 2001). Proponents maintain that communities with high species diversity will contain many species with slightly different resource usage, creating an environment in which the community utilizes a larger portion of available resources. Under these conditions, few resources are available for the invasion of a new species (MacArthur 1970, 1972). In order to invade successfully, a species' resource requirements must be lower than those of a native species (Tilman 1982). Lower species diversity should leave a larger portion of the system's resources unutilized.

Recently, observational data (Levine & D'Antonio 1999) have yielded support for a competing view: those communities that support high native biodiversity possess the necessary resources to support large numbers of invasive species (Lonsdale 1999; Stohlgren et al. 1999). Highly productive ecosystems containing abundant niche space may see frequent extinction and establishment of species, increasing the likelihood of colonization by an invasive (May 1973).

Smith et al. (2004) found that dominance, not diversity better prevented the spread of invasives. They concluded that communities in which one or a few species are dominant could better utilize the available nutrients than a larger number of less dominant species. Smith et al. (2004) demonstrated experimentally what Tilman et al. (1997) had theorized: artificially constructed, higher diversity communities are more likely to contain a dominant species able to sequester available resources. A dominant species, whether it is in monoculture or exists with many species, would wield the greatest influence on community invasibility (Crawley et al. 1999). Communities possessing one or a few highly dominant species also tend to have lower diversity than those with lower dominance (Smith et al. 2004). The importance of dominance may explain the different relationships between diversity and invasibility observed (Huston 1997, Tilman 1997). As the number of species in a community increases, the probability of possessing the most resistant species increases. This sampling effect (Aarssen 1997; Huston 1997) asserts that low diversity communities, by chance tend to lack the most resistant species. Any correlation between diversity and invasibility is merely a statistical artifact.

Most studies manipulating diversity on small scales have found a negative correlation between diversity and invasibility (Levine 2000; Dukes 2002). These studies have sought to control for outside factors such as soil nutrient and water content (Naeem et al. 2000; Prieur-Richard et al. 2000) by randomly assembling communities of different composition and diversity levels. Unfortunately these experiments rarely contain the most dominant or invasion-resistant species in enough of the lower diversity assemblages to

overcome sampling effects (Wardle 2001). A lack of controlled, manipulative studies addressing the role of biodiversity in preventing invasions has made it difficult to disentangle the effect of biodiversity itself from the effects of environment, productivity, and the individual roles of dominant species. Recently Davies et al. (2005) demonstrated that much of the scale-dependent invasion paradox (Fridley et al. 2007) could be explained by differences in resource heterogeneity between scales. At the neighborhood scale, resources are uniform enough to prevent much niche differentiation. On larger community or regional scales, there is enough resource heterogeneity to allow greater niche differentiation. Thus high gamma diversity (Whittaker 1972) may indicate the presence of many niches for a non-native species to exploit.

Disturbances have also been implicated in many invasions worldwide (e.g., Hobbs & Atkins 1988; Burke & Grime 1996; Vitousek et al. 1997). The fluctuating resource hypothesis (Davis et al. 2000) was proposed to explain some of these disturbance-moderated invasions. The theory states that undisturbed communities tend to utilize all available resources. In this scenario invasions are most likely to occur when the utilization of a limiting resource declines, usually through increased supply of the resource or disturbance (Davis & Pelsor 2001). Disturbances often reduce community biomass, creating a situation in which there is less demand for once-limiting resources. Invasive plants frequently are ruderal species (Baker 1986), thriving on disturbance and growing quickly under high resource conditions (Grime 1979).

Nutrients pulses have also been shown to facilitate invasions in a variety of ecosystems (Morghan & Rice 2006; Olson & Blicher 2003). Morghan and Rice (2006)

found that low resource sites with rocky soils contained fewer invasive plants than more productive sites in California grasslands. However, these resource-limited sites were invaded more frequently during wet years. The fertilization of native-dominated serpentine grasslands in California quickly caused a shift in composition toward invasive species (Huenneke et al. 1990; Thomsen et al. 2006). The introduction of carbon to deplete soil nitrogen has been used to decrease the competitive advantage of ruderal invasives in grasslands (e.g., Wilson & Gerry 1995; Alpert & Maron 2000; Corbin & D'Antonio 2004). Although studies on the relationship between resource variation or diversity and invasibility have been widespread, Maron and Marler (2007) were the first to examine explicitly the interaction between these important mechanisms. They found high diversity resisted invasion of *Centaurea maculosa* regardless of resource level. Human habitat modification, (especially fertilization) and the alteration of fire and hydrologic regimes, has increased nutrient supplies to many naturally nutrient-poor habitats, facilitating invasion by plants with lower resource-use-efficiency and faster growth rates (Vitousek et al. 1997; Lowe et al. 2003).

Fire is essential to the persistence of many ecosystems, especially tallgrass prairies. In grasslands fire halts shrub encroachment, but may also facilitate invasion. Fire may release nutrients sequestered in plant tissue as a nutrient pulse that increases post-fire NPP (Turner et al. 1997). Frequently burned sites exhibit low nutrient conditions due to the continued volatilization of nitrogen and litter loss (Wilson & Shay 1990). Infrequent fire removes the litter layer, creating a high light condition beneficial to germination. In periodically burned grasslands, increased ANPP might be associated with

a shift from pre-fire light limitation to post-fire nitrogen limitation (Blair 1997). This transient maximum of ANPP, when the system is limited by neither light nor nitrogen could facilitate establishment by exotic species. MacDougall (2005) found that low diversity oak savanna was more easily invaded following fire than high diversity savannas. This study highlights the importance of interactions between diversity and disturbance in natural systems. Although fire is useful in preventing shrub encroachment, once shrubs become established and are large enough to withstand fire, the post-fire resource pulse can increase shrub biomass production (McCarron & Knapp 2003).

Mesic prairies are native to Virginia and extend into the Midwestern United States. This habitat features several large C₄ grasses (Virginia Natural Heritage 2001). *Andropogon gerardii* and *Sorghastrum nutans* dominate these communities, along with *Panicum virgatum* and *Schizachyrium scoparium* to a lesser extent (Smith & Knapp 2001). Since these grasses possess the C₄ photosynthetic pathway, they have higher water and nutrient-use-efficiency (NUE) than C₃ plants (Knapp 1985a; Seadstedt et al. 1991). Their higher NUE allows C₄ grasses to have substantially lower leaf nitrogen concentrations. When their leaves senesce, the leaf litter is also lower in nitrogen, promoting a low-nutrient environment (Wedin 1995). The high nutrient-use-efficiency of the dominant warm-season grasses may explain their dominance under low nutrient conditions (Smith & Knapp 1999, Fargione et al. 2003) but may also leave tallgrass prairie vulnerable to invasion by less efficient C₃ species if resource levels become more abundant. Increasing fertilization, especially in agricultural areas (Galloway et al. 2004), may lead to a competitive shift to less efficient species as the tallgrass prairie landscape

becomes more fertile (Stevens et al. 2004). Human habitat alteration may be facilitating this decline by increasing fertilization and altering natural disturbance regimes, actions that favor faster growing non-native species.

This study will examine the effects of grass diversity and nutrient disturbances in an experimental tall-grass system in Virginia that is being invaded by an aggressive, perennial C₃ forb, *Galium verum*. The dominant warm-season grasses of the tallgrass prairie differ physiologically from *Galium* in several important respects. These differences may allow the species to respond to disturbances differently. The diversity of native species may also play a role in the establishment and success of exotic species. In this study I sought to answer three questions:

- 1) Does soil nutrient condition affect *G. verum* success in tallgrass prairie?
- 2) Does high native biodiversity impede the invasion of mesic grasslands by *G. verum*?
- 3) How does early-season fire affect the growth and reproduction of *G. verum*?

Methods

Galium verum

Before restoration, *Galium verum* (Rubiaceae) dominated the Blandy meadow. It persists in the meadow, although it is less prevalent. *G. verum* is an herbaceous plant of European origin that possesses the C₃ photosynthetic pathway (Liu et al. 2004). The species has very narrow leaves in whorls of 6 or 8 and densely clustered 4-petaled, yellow flowers that are approximately 2 – 3 mm in diameter (Newcomb 1989). Stems of *G. verum*

can reach 1 meter in height and often achieve very high density locally. *G. verum* was first collected at Blandy in the 1920s and is especially prevalent in disturbed areas and roadsides of the Shenandoah Valley of Virginia (personal observation). The species flowers in late June and sets seed by mid-August (personal observation). According to the USDA (USDA 2008), *G. verum* is naturalized through much of the United States and Canada (north of Tennessee, Arkansas and Oklahoma). Based on its spread through the Shenandoah Valley, this is likely a species of emerging concern (personal observation).

Study Site and Diversity Treatments

The ~14-hectare native grass meadow at Blandy Experimental Farm in Boyce, VA (39°5'35"N, 78°3'33"W) is divided into replicated plots of each of five native warm-season grass species compositions. Three of these five native grass combinations were used in this study: C1 (*Andropogon gerardii*), C3 (*A. gerardii*, *Schizachyrium scoparium* and *Andropogon virginicus*) and C5 (*A. gerardii*, *S. scoparium*, *A. virginicus*, *Sorghastrum nutans* and *Panicum virgatum*). *A. gerardii* is the most dominant species of the tallgrass prairie and consequently the most relevant to study.

This meadow was established in 2000. In Fall 1999, glyphosate herbicide (Roundup®) was applied to the existing vegetation. Roundup was reapplied in the spring of 2000 followed by a burn. In May 2000 6 lbs. of “pure, live seed” per acre were sown into each diversity assemblage. Seed from each species was represented equally by weight in the multi-species mixes (i.e., the C3 and C5 diversity treatments). These species combinations were established in a randomized complete block design, with three blocks arranged perpendicular to the slope gradient. The upslope section is referred to as

the 'xeric' block. The 'mesic' block is at midslope and the 'hydryc' block is at the lowest elevation. The meadow was left unburned until the xeric site was burned in 2003. It was burned again in Spring 2007 and was not included in this experiment. The mesic block was last burned in 2004, while the hydryc block was last burned in 2006.

In March, 2007 48 1m x 1m plots were established within the mesic and hydryc sections of the meadow. Within both the hydryc and mesic blocks, I established two replicates of each of four experimental treatments within each diversity regime. Each plot contained *Galium verum*. One of the native grasses (*A. virginicum*) was uncommon in the experiment and therefore was missing from many of the three- and five-species plots (i.e., C3 and C5 treatments).

Nutrient Manipulations

Nutrient manipulations included depleted soil nitrogen (N1), ambient soil nitrogen (N2), elevated soil nitrogen (N3) and a controlled burn (N4). Nitrogen depletion was performed with sawdust addition. These manipulations were assigned randomly to each of the four plots within each replicate. Sawdust is a high C:N ratio substrate, resulting in net immobilization of soil nitrogen (Corbin & D'Antonio 2004). I added 400 g/m² sawdust (Wilson & Gerry 1995). Ambient soil nitrogen (N2) plots were left unmanipulated. Nitrogen was added in the form of Osmocote at 30 g/m² N (Foster & Gross 1998). Osmocote is a slow-release fertilizer that produced temporally uniform nitrogen conditions. This degree of fertilization has evoked a strong response from C₃ species (Wedin & Tilman 1993). I performed plot-sized burns (N4) by surrounding recipient plots with a 4ft x 4ft x 4ft plywood box lined with aluminum roof flashing and

setting fire to the vegetation. These burns were performed on May 3 and May 8, 2007. The box was large enough to allow several centimeters outside the plot to be burned, preventing edge effects from encroaching upon the plot. All vegetation was left in place and undisturbed after burning. Fertilizer and sawdust were added May 9, 2007.

Vegetation censusing

On June 5, July 24 and September 2, 2007 I censused *G. verum* stems. Due to the high density of *G. verum* in many plots, I divided each 1m x 1m quadrat into 25 0.04m² cells. 5 cells were chosen randomly for each plot and stems within these cells was counted. From July 22 – 24 and September 8 - 9, 2007 the total tillers of all warm-season grasses were counted.

Vegetation harvest

All aboveground biomass was harvested from plots following the first frost in late October. Biomass was separated by species for target species (i.e., individual warm-season grass species and *Galium*). Other biomass was separated into “Other forbs” and “Other grasses”. Samples were dried at 50°C and weighed.

Reproductive output

G. verum reproductive output was estimated by harvesting 10 flowering stems randomly from each plot. All flowering stems were harvested if the plot contained fewer than 10 reproductive plants. Seeds were separated from stems and weighed.

Soil nutrient testing

Plant-available soil ammonium (NH₄⁺) and nitrate (NO₃⁻) concentrations were evaluated using Western Ag PRSTM-probes (Western Ag Innovations Inc., Saskatoon,

SK, Canada). PRSTM-probes were buried for two 16-day spans, July 7 – 23, 2007 and August 23 – September 9, 2007 (hereafter referred to as the September burial). Since PRSTM-probes have a weaker affinity for soil nitrate and ammonium than plant roots, 15 cm lengths of 8 cm diameter PVC-pipe were installed in plots. These root exclusion cylinders prevented differences in root density from biasing measurements of plant-available nitrogen. Root exclusion cylinders were installed randomly within plots and all vegetation from within the cylinder was removed. Cylinders were installed one day prior to the July PRSTM-probe burial and relocated before the September burial. 500 mL of water was added to soften the soil prior to cylinder installation.

Soil moisture

Soil moisture was measured by extracting a 15 cm core of soil and dividing it into two pieces, the top 5 cm and the next 10 cm of soil. Soil samples were taken on June 7, 2007 and twice during each PRSTM-probe burial period. The samples were dried to constant mass at 65°C. Percent soil moisture was calculated as:

$$[(\text{Wet mass of soil} - \text{dry mass of soil}) / \text{Wet mass of soil}] \times 100.$$

Percent soil moisture from these five sampling dates was analyzed as a single measure, the average soil moisture over this period.

Statistical Analyses

Total above-ground biomass and reproductive measures were analyzed as a split-plot ANOVA with diversity treatment as the whole-plot effect and nutrient treatment as the sub-plot effect using Proc Mixed in SAS (SAS Institute Inc., Cary, NC, Version 9.1). Biomass of all native grass species was combined to yield a single value of warm-season

grass biomass per plot. Relative species biomass was also calculated. Individual *Galium* censuses, warm-season grass censuses and plant-available nitrogen were analyzed as split-plots with diversity as the whole-plot effect and nutrient treatment as the split-plot in SAS Proc Mixed. In addition to separate analyses for each measurement date, repeated-measures ANOVA were performed using SAS Proc Mixed.

Results

Nutrient Effects

Soil Nutrients

As expected, the fertilized plots had the highest plant-available N levels in both July and September (Figure 10a). In July burned plots had significantly higher plant-available N than either the control or depleted N treatments (Table 5a). By the September incubation, however, total N in burned plots had decreased so that there were no differences among depleted, ambient and burned plots (Table 5d). Both burned and fertilized plots exhibited decreases in plant-available N throughout the summer, while depleted and ambient N conditions increased slightly. Depleted and ambient N exhibited remarkably similar soil N levels, indicating that sawdust addition may have only slightly depleted soil N.

Plant-available NO_3^- (Figure 10b) exhibited the same trends as total plant-available N. Fertilized plots had significantly higher concentrations than any other treatment and in July, burned plots had significantly higher levels of NO_3^- than either ambient N or depleted N treatments (Table 5b). By September, burned plots were not

significantly different from ambient and depleted N in soil NO_3^- (Table 5e). Again, a trend of decreasing NO_3^- occurred for burned and fertilized treatments. The results for plant-available NH_4^+ were slightly different (Table 5c). Fertilized plots had the highest NH_4^+ concentrations in both July and September (Figure 10c).

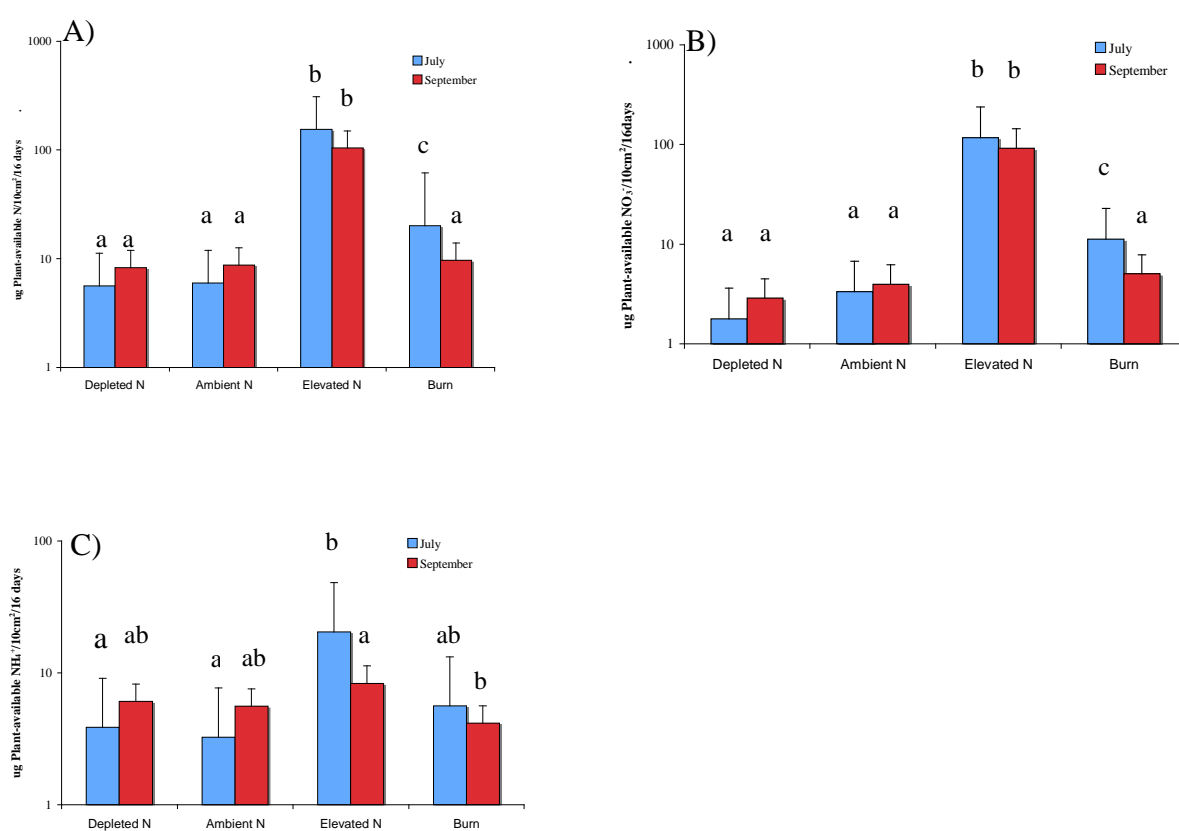


Figure 10. Plant-available soil nitrogen concentrations for each nutrient condition ($\mu\text{g N}/10\text{cm}^2/16\text{ days}$) (mean + 95%CL) during July and September incubations. **A)** Total plant-available N, **B)** Plant-available NO_3^- , **C)** Plant-available NH_4^+ . Shared letters for the same incubation period denote no significant difference at $p = 0.05$. Pairwise comparisons were performed using the Tukey-Kramer test.

However, in September NH_4^+ in fertilized plots was significantly greater than burned plots only (Table 5f). Neither ambient nor depleted N treatments had soil NH_4^+ concentrations that were significantly different from elevated N.

Warm-Season Grasses

There was a significant effect of nutrient treatment on warm-season grass biomass (Table 6a). Burned plots produced significantly less warm-season grass biomass than any unburned treatment (Figure 11a). Interestingly, there was no difference in warm-season grass biomass between elevated and depleted N conditions. All unburned treatments generated mean biomass of more than 500 g/m^2 , while the mean biomass production for burned plots was less than 300 g/m^2 (Figure 11b). When the production of *A. gerardii* was considered separately from other grasses, there was still a significant nutrient effect (Table 6c). *A. gerardii* responded similarly to total warm-season grasses by producing significantly less biomass in burned plots than unburned plots (Figure 11d).

Warm-season grass tiller density in both July and September were also significantly affected by nutrient manipulation (Table 6d,e). Plots receiving a burn had the highest density of warm-season grass stems during both July and September (Figure 11c) (411 tillers/m^2 and 263 tillers/m^2 , respectively). In July the elevated N treatment had significantly fewer stems than depleted N and burned plots. Burned plots possessed significantly greater stem density than control and fertilized plots in September. Fertilized plots had the lowest stem density during both samples. Depleted N plots had significantly greater stem density than elevated N treatments in both July and September. Using repeated-measures ANOVA, I found no nutrient treatment*time interaction (Table 7a).

All four treatments responded similarly throughout the summer. Warm-season grass tiller density declined substantially through the summer, apparently due to competition for resources (Table 7a).

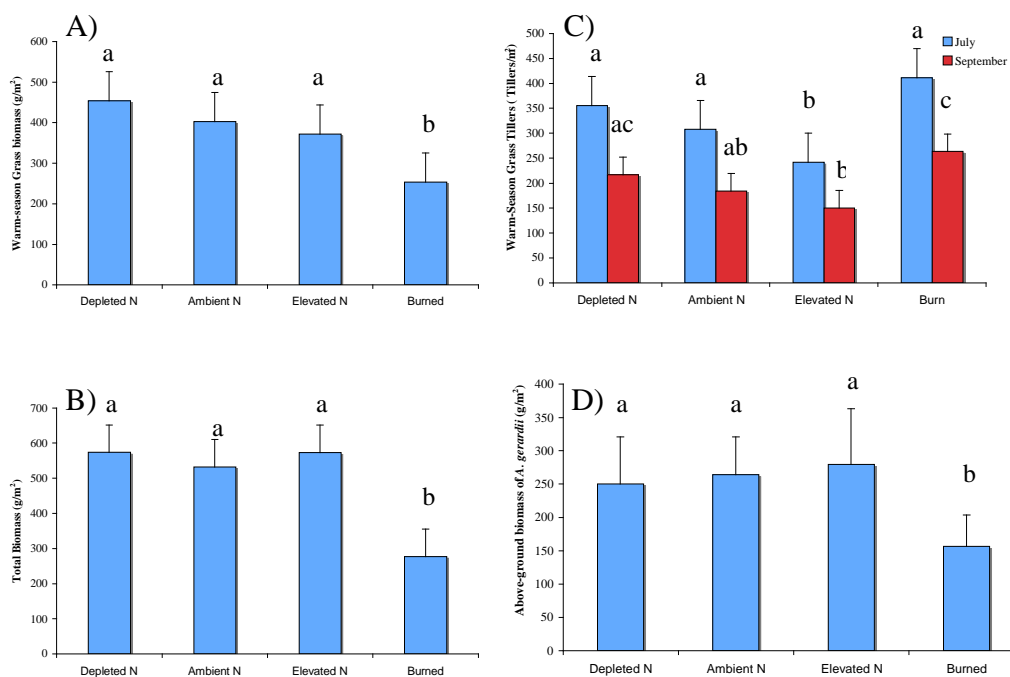


Figure 11. Warm-season grass analyses for nutrient treatments **A)** All warm-season grass biomass (g/m²) harvested in November 2007. **B)** Total plot biomass (sum of all grasses and all forbs) of each nutrient manipulation. **C)** Warm-season grass tiller density in July and September. **D)** Above-ground biomass of *A. gerardii* (g/m²) harvested in November 2007. Shared letters denote no significant difference at $p = 0.05$. Pairwise comparisons were performed using the Tukey-Kramer test. Error bars denote 95% CL.

Galium verum

Galium biomass differed significantly based on nutrient treatment (Table 8a).

Fertilizer significantly increased *Galium* biomass over all other treatments, while fire reduced biomass significantly (Figure 12a). Burned plots contained only 8.25g/m² of

Galium biomass, while both depleted N and ambient N produced several times more *Galium* biomass (56.99 g/m² and 60.24g/m², respectively). More than twice as much *Galium* occurred in fertilized plots (123.49 g/m²) as in any other treatment. Depleted and ambient N had similar production of *Galium*. Although burned plots yielded the least *Galium* biomass, this treatment had comparable *Galium* stem densities to both depleted N and ambient N (Figure 12b). Fertilized plots had the greatest density of *Galium* on all sampling dates, although stem density was significantly greater than all other treatments only in September (Table 8d,e,f). There was a significant time effect on *Galium* stem density, with all plots decreasing in *Galium* density over the growing season (Table 7b). There was also a significant nutrient*time interaction. Burned plots had similar *Galium* densities in June but declined precipitously by the July census (Figure 12b). Fertilized plots maintained high *Galium* density throughout the study.

Burning significantly hindered *Galium* reproductive output (Table 8b). Unburned plots regardless of treatment had similar numbers of reproductive *Galium* plants while most burned plots had no seed production (Figure 12c).

Both total plot biomass (all forbs and grasses) (Table 6c) and *Galium* biomass declined in burned plots relative to unburned treatments. However, *Galium* made up a significantly smaller portion of burned than any unburned treatments (Table 8b). *Galium* contributed 28.8% of the total biomass in fertilized plots, while in burned plots only 4.6% of the total biomass was *Galium* (Figure 12d). Depleted N and control treatments had similar percentages of *Galium* (14.8 and 15.9%, respectively).

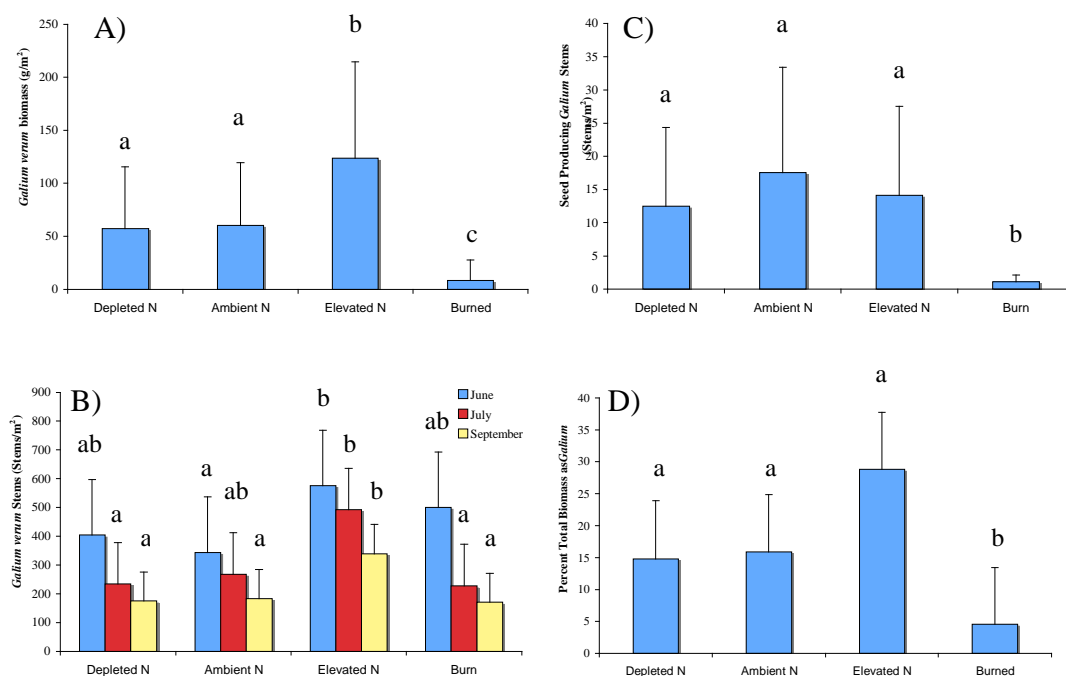


Figure 12. *Galium verum* analyses for nutrient treatments. **A)** *Galium verum* biomass (g/m^2) harvested in November 2007. **B)** *Galium* stem density (stems/m^2) measured in June, July and September. **C)** Number of *Galium* stems producing seed per 1m^2 plot. **D)** Percentage of total biomass (grass + forbs) composed of *Galium verum*. For all analyses, similar letters denote no significant difference at $p = 0.05$. All error bars represent mean + 95% CL.

Soil Moisture

I found no effect of nutrient manipulation on soil moisture content in either the top 5 cm or the 5 – 15 cm section of soil (Table 9, Figure 13).

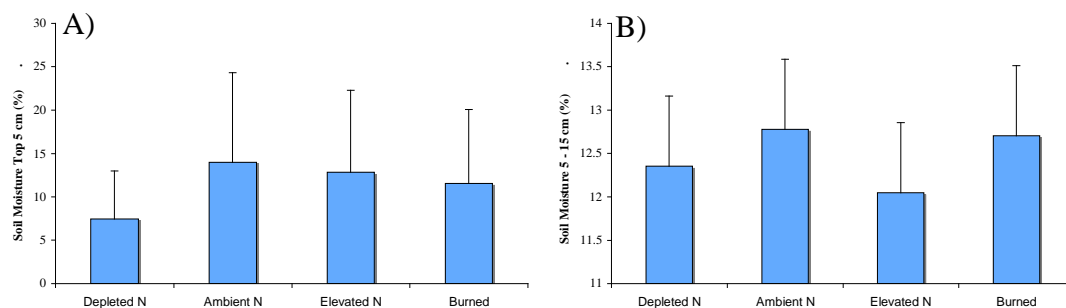


Figure 13. Mean soil moisture from five sampling dates throughout summer 2007 for each nutrient treatment. **A)** Percent soil moisture in the top 5cm of soil. **B)** Percent soil moisture in the 5 – 15cm layer of soil. There were no significant differences in soil moisture among nutrient treatments in either soil layer ($p = 0.38$, $p = 0.51$, respectively).

Diversity Effects

Soil Nutrients

Native grass diversity had no effect on plant-available total N (Figure 14a) during either incubation (Table 5a,d). I saw no differences among diversity levels in plant-available NO_3^- (Figure 14b) in July or September (Table 5b,e). There were no significant interactions based on repeated-measures ANOVA among time, diversity and nutrients on plant-available N, NO_3^- or NH_4^+ . In September, plant-available NH_4^+ was significantly more abundant in one-species plots than in three-species plots (Figure 14c). Five-species plots did not have significantly different concentrations of NH_4^+ from either diversity treatment (Table 5f). There was no significant effect of species diversity on July NH_4^+ concentration (Table 5c). Contrary to soil nitrogen concentrations in nutrient treatments, total plant-available N, NO_3^- and NH_4^+ all responded similarly within a single diversity level. One-species plots decreased in plant-available total N, NH_4^+ and NO_3^- from July to September. Three-species plots increased over this same interval and five-species plots remained quite constant.

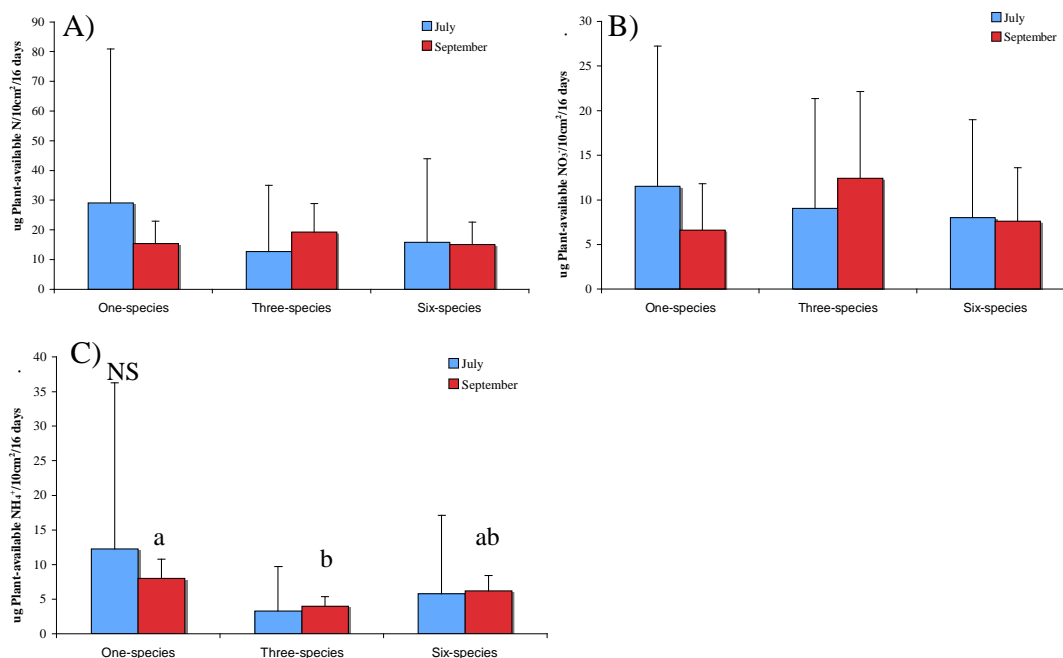


Figure 14. Plant-available soil nitrogen concentrations for each diversity level ($\mu\text{g N}/10\text{cm}^2/16\text{ days}$) (mean + 95%CL) during July and September incubations. **A)** Total plant-available N. **B)** Plant-available NO_3^- , **C)** Plant-available NH_4^+ . The only significant effect of diversity level occurred on NH_4^+ during the September incubation. Shared letters for this incubation denote no significant difference at $p = 0.05$. Pairwise comparisons were performed using the Tukey-Kramer test. No other diversity effects were significant at $p = 0.05$.

Warm-Season Grasses

I found no effect of diversity treatment (1, 3 or 5 native warm-season grasses) on biomass production of warm-season grasses (Figure 14a). Warm-season grass biomass (Table 6a) differed little among the three diversity levels. Plots containing *A. gerardii* (one species) had the greatest grass production, but this difference was not significant. However the mean warm-season grass tiller density in July was significantly higher in one-species than in five species plots (Table 6d), but this trend was not evident in September (Table 6e) (Figure 14b). There was a marginally significant effect of diversity

when tiller density is analyzed with repeated-measures ANOVA (Table 7a) but there was no diversity*time interaction on tiller density. In other words, tiller density declined from July to September but all diversity levels exhibited similar declines.

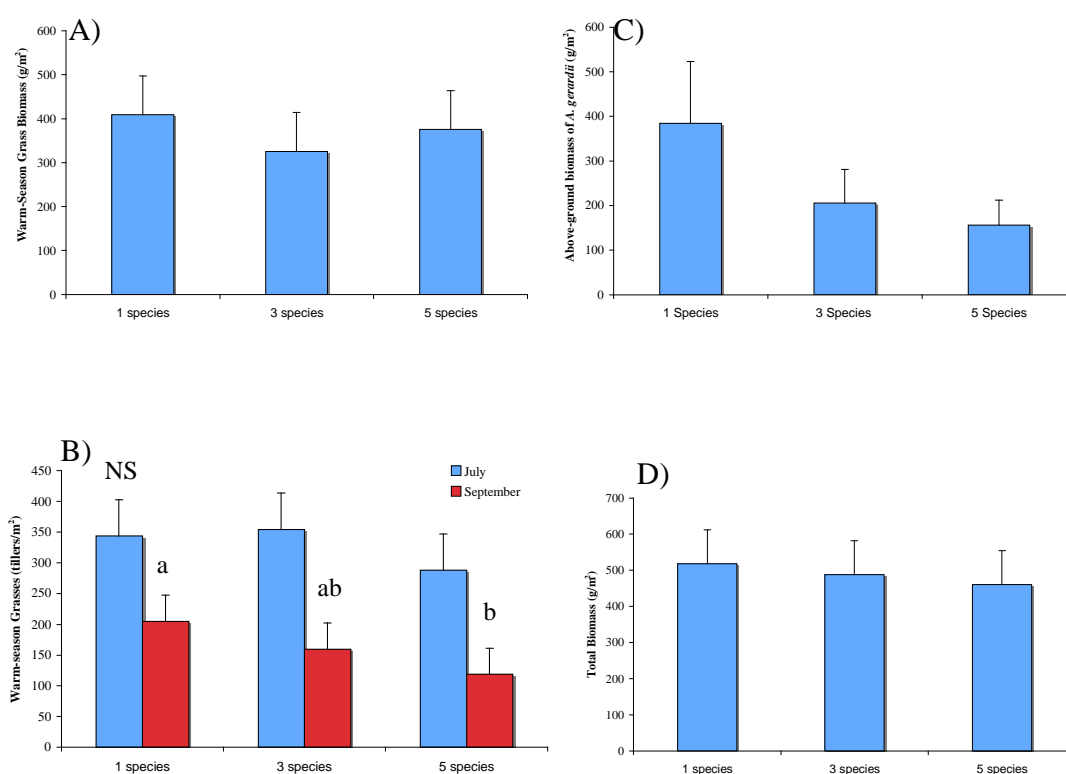


Figure 15. Warm-season grass analyses for diversity levels **A)** All warm-season grass above-ground biomass (g/m^2) harvested in November 2007. **B)** Warm-season grass tiller density in July and September (tillers/m^2). **C)** Above-ground biomass (g/m^2) of *A. gerardii* harvested in November 2007. Warm-season grass tiller density in September and total *A. gerardii* biomass exhibited significant diversity effects. **D)** Total plot biomass (sum of all grasses and all forbs) of each diversity treatment. Shared letters denote no significant difference at $p = 0.05$. Pairwise comparisons were performed using the Tukey-Kramer test. Error bars denote 95% CL. Native grass diversity did not significantly affect warm-season grass biomass or July tiller density.

When *A. gerardii* was considered separately from total warm-season grass biomass, there were significant biomass differences among diversity levels (Table 6b). In one-species plots, *A. gerardii* production was highest (384.13 g/m²) and declined substantially when grown with two or four other species (206.03 and 156.02 g/m², respectively) indicating that there was competition among native grasses and over-yielding did not occur (Figure 14c).

Total plot biomass (the sum of *Galium*, native grass, and all other grasses and forbs) was nearly identical (Table 6c) across all diversity levels (Figure 14d) indicating that there was no increase in total net primary production with increasing diversity.

Galium verum

I found no evidence for effects of native diversity on community invasibility or increased productivity of *G. verum*. *Galium* stem density did not differ among diversity levels in June, July or September (Figure 16b). There was, however, a significant diversity*time interaction for *Galium* stem density (Table 7b). In one-species plots *Galium* density declined substantially between June and July but there was very little change between July and September. Three and five-species plots exhibited a more gradual decrease in *Galium* density through the growing season.

Increasing native diversity did not inhibit *Galium* biomass production (Figure 16a). Seed production was also similar across all diversity levels (Figure 16c). Similarly *Galium* made up similar percentages of total biomass at all diversity levels (Figure 16d). Unlike nutrient manipulations, diversity had little effect on the number of *Galium* stems, its biomass or reproduction.

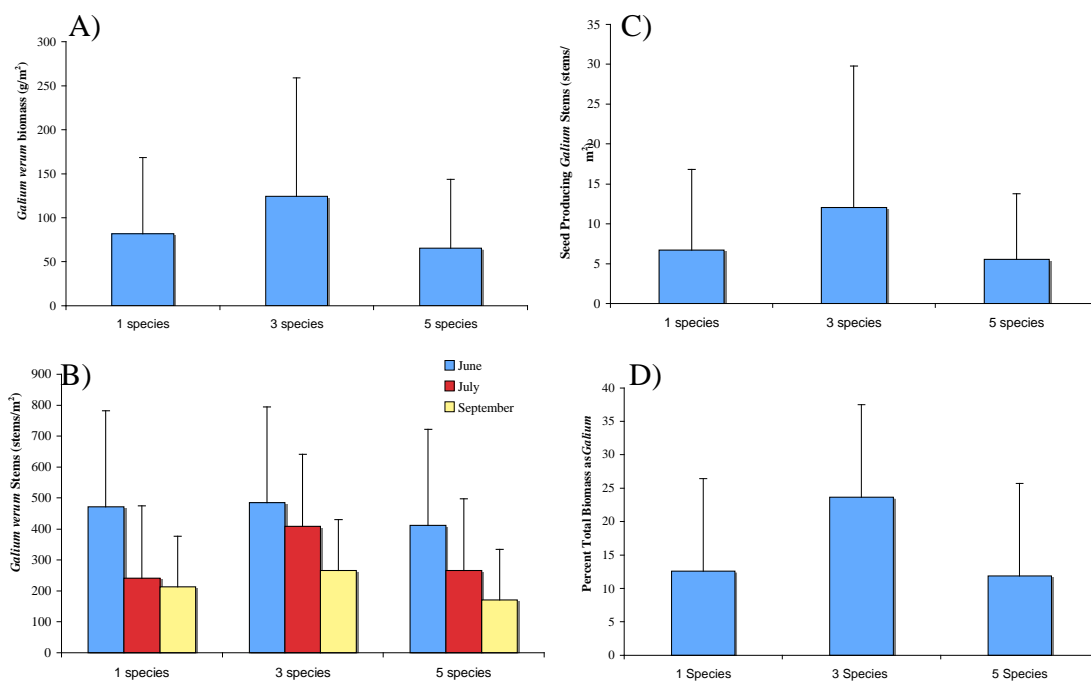


Figure 16. *Galium verum* analyses for diversity levels. **A)** *Galium verum* biomass (g/m²) harvested in November 2007. **B)** *Galium* stem density (stems/m²) measured in June, July and September. **C)** Number of *Galium* stems producing seed per 1m² plot. **D)** Percentage of total biomass (grass + forbs) composed of *Galium verum*. There was no effect of native species diversity on any response variable at $p = 0.05$. All error bars represent mean + 95% CL.

Soil moisture

Native grass diversity had no effect on soil moisture content in this experiment (Table 9, Figure 17).

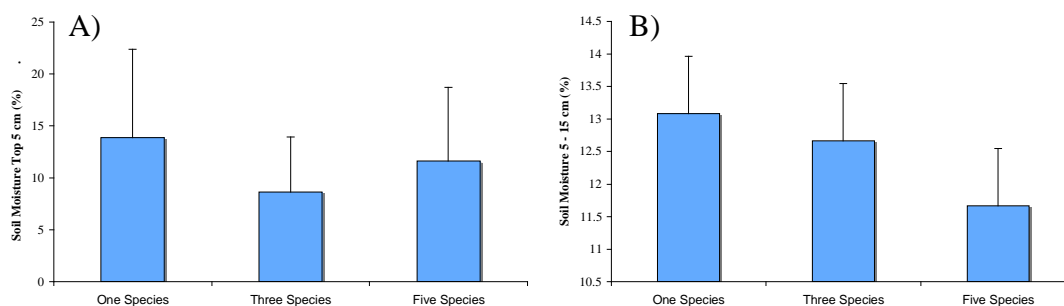


Figure 17. Mean soil moisture (mean + 95% CL) from five sampling dates throughout summer 2007 for each diversity treatment. **A)** Percent soil moisture in the top 5cm of soil. **B)** Percent soil moisture in the 5 – 15cm layer of soil. There were no significant differences in soil moisture among diversity treatments in either soil layer.

*Diversity*Nutrient Effects*

Soil Nutrients

There was a significant diversity*nutrient interaction among treatments on total plant-available N during the September incubation (Table 5d). Fertilized plots showed a substantial increase in total plant-available soil nitrogen from one to three species plots and a slight decline from three to five species. The other three treatments (depleted N, ambient N, burned) had similar soil nitrogen concentrations at all levels of native diversity (Figure 18). This interaction was not apparent when looking at NO_3^- or NH_4^+ separately, however (Table 5e,f). There were no significant interactions between diversity and nutrient treatment for total N, NO_3^- or NH_4^+ during the July incubation (Table 5a,b,c).

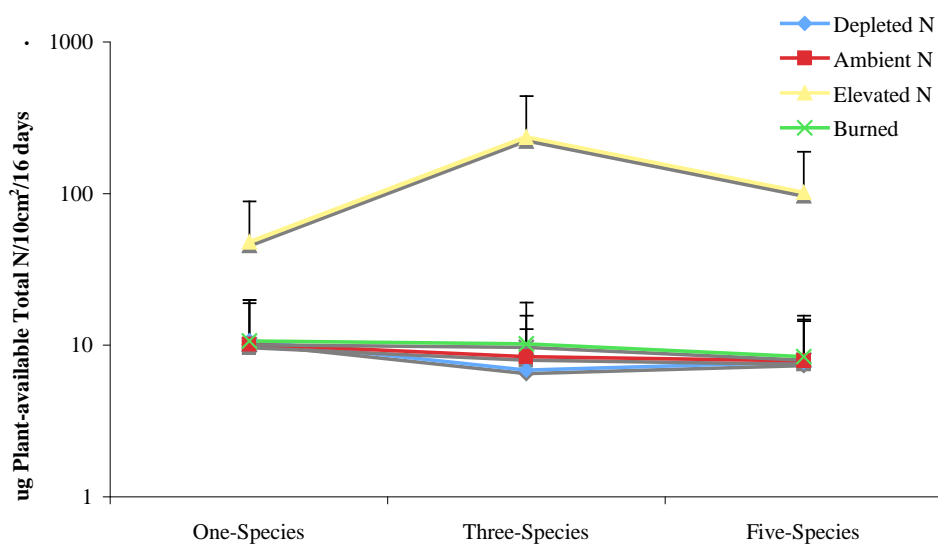


Figure 18. Diversity*Nutrient interaction for total plant-available soil N during the September incubation period. This interaction was significant ($F_{6,27} = 2.57$, $p = 0.04$) though neither NO_3^- nor NH_4^+ exhibited a significant diversity*nutrient interaction during this incubation period.

Warm-Season Grasses

Different levels of native grass diversity responded similarly to nutrient treatments with respect to warm-season grass biomass (Table 6a). There was no significant diversity*nutrient interaction for either July or September warm-season grass tiller density (Table 6d,e).

Galium verum

The interaction between diversity and nutrient treatment was insignificant for *Galium* biomass (Table 8a). However, there was a significant diversity*nutrient treatment interaction in July *Galium* stem density (Table 8e). Depleted and ambient N plots showed a peak in *Galium* stem density in three-species plots and a substantial decline in five-species plots (Figure 19). In both fertilized and burned plots, there was an increase in

Galium stem density from one to three-species, but no decline in five-species plots, indicating that higher soil nitrogen levels decreased the inhibitory effect of high species diversity on *Galium* stem abundance. Neither June nor September stem densities had significantly different nutrient effects on different native grass diversity levels (Table 8 d,f).

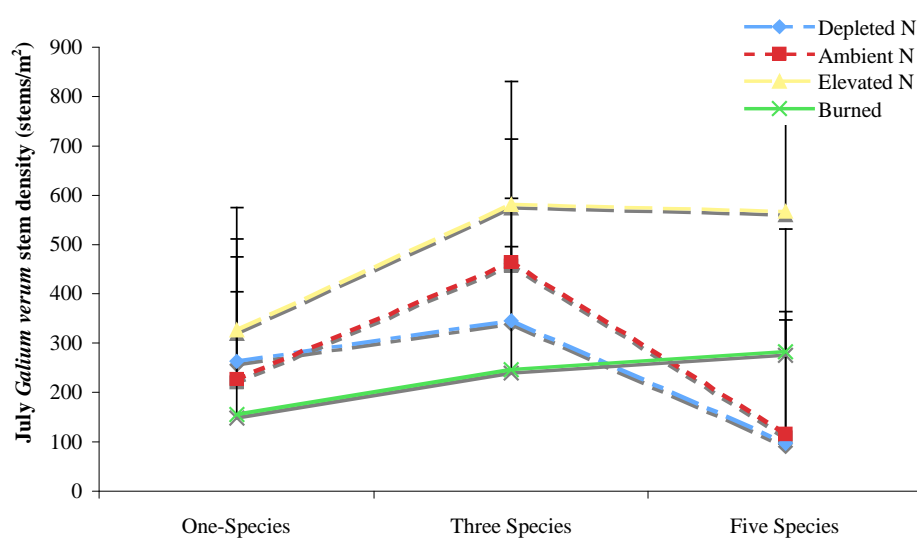


Figure 19. Diversity*Nutrient interaction for July *Galium* stem density. This interaction was significant ($F_{6,27} = 3.21$, $p = 0.017$) although neither June nor September *Galium* stem densities exhibited a significant nutrient*diversity interaction.

Soil moisture

Soil moisture in the three diversity levels did not differ based on nutrient manipulations employed. There were no diversity*nutrient interactions with regard to either the top 5cm of soil or the 5-15cm soil layer (Table 9a,b).

Discussion

I found strong support for the fluctuating resource hypothesis in this study. According to this theory communities are most susceptible to invasion when excess nutrients are introduced to the system (Davis et al. 2000). These nutrients can be utilized by invasive species that would otherwise be unable to establish in a community with few unsequestered nutrients. Excess nutrients (fertilized plots) allowed *Galium* to achieve its highest level of success. In control and depleted nitrogen plots, the low nutrient levels helped the native community resist *Galium* invasion. Even though fire produced a nutrient pulse, the physical disturbance associated with fire may have decreased *Galium* success in this experiment.

Although nutrients and disturbance appear to have had a large impact on *Galium* success at Blandy, the effects of diversity were much less convincing. I found very few effects of diversity, positive or negative, suggesting that in this system, native community diversity is less important than ecosystem characteristics (resource levels and disturbance) in explaining *Galium* success.

Nutrient Effects

Galium clearly utilized nitrogen pulses more efficiently than the dominant warm-season grasses. This has important implications for the management and restoration of tallgrass prairie habitat, much of which exists in heavily agricultural areas. C₄ species are less competitive under high nitrogen conditions and may become suppressed by lower NUE species (Wedin & Tilman 1993). In my study there were no significant differences in C₄ grass biomass among any of the unburned treatments, suggesting that warm-season

grasses could not respond to increased nitrogen availability. Similarly, Silletti et al. (2004) also demonstrated that *A. gerardii* responded little to nitrogen addition. Low NUE ruderal species like *Galium* are better able to utilize nutrient pulses and grow more rapidly under high resource conditions (Grime 1979) leading to the competitive exclusion of slow-growing, high NUE species (e.g., Gross et al. 2005; Lenz & Facelli 2005; Gendron & Wilson 2007). In fact, lowering soil nutrient levels is a commonly used method to combat fertilization-related invasions of naturally nutrient poor ecosystems (Wilson & Gerry 1995; Alpert & Maron 2000; Blumenthal et al. 2003).

Temporal niche differentiation could be important for the invasion of *Galium* into this C₄-dominated prairie. C₄ plants are more efficient at higher temperatures and light levels (Edwards & Still 2008). As a result, C₄ species are most productive during the summer, while C₃ species tend to grow most in cooler months (spring and fall) (Yuan et al. 2007). This early nutrient pulse may have been initially more readily available to cool-season species. Spring nutrient inputs may shift competition more completely in favor of invasive species than similar pulses occurring during summer.

My efforts to create a low N environment were equivocal. The depleted nitrogen condition differed little from the control in plant-available soil nitrogen content, species composition or abundance over the growing season. Several possible explanations exist. The sawdust addition may have been insufficient to cause a large microbial nitrogen immobilization or the effect of sawdust may not have lasted the entire growing season. Since the 2007 growing season was particularly dry, there may not have been enough soil moisture for the soil microbial community to utilize the abundant carbon and produce a

vigorous response (Jensen et al. 2003; Anaya et al. 2007). It would be interesting to see if the C₄ grasses would be able to exclude *Galium* at N levels lower than those I was able to examine.

Fire as a Nutrient Input and Disturbance

Burned plots displayed a unique combination of responses. *Galium* biomass was highly suppressed in burned plots, yet stem density was comparable to both depleted N and ambient N treatments. Although fire strongly inhibited *Galium* biomass production, it did not eliminate many plants. In the future these plots may respond similarly to plots that had not been burned. Burning reduced flowering in *Galium*, but it is unclear how dependent this species is on sexual reproduction for persistence and spread. If this species spreads via seed, then fire will have a much stronger inhibitory effect on *Galium* than if it spreads clonally.

Fire is sometimes used to control invasive species (e.g., DiTomaso et al. 1999, Buckley et al. 2007, Simmons et al. 2007, Davies et al. 2008). In other situations fire can exacerbate the invasive species problem (D'Antonio 2000). Dormant season burns frequently enhance productivity, while growing season burns inhibit growth (Howe 1994). Early fire may harm C₃ forbs more than C₄ grasses because cool-season species typically begin to grow before the fire, while warm-season species do not often grow until later, when they are able to utilize the nutrient pulse. Spring fire effectively hindered *Centaurea maculosa* spread and enhanced the dominance of warm-season grasses in Michigan (MacDonald et al. 2007). Emery and Gross (2005) found that only summer burning reduced population sizes in *Centaurea maculosa*, indicating that physical

damage to plants while growing may suppress invasive forbs the most. *Galium* growth commences much earlier than warm-season grasses (personal observation), and the timing of the burn in this study likely inhibited *Galium* more than the native grasses. Although fire may prevent *Galium* from dominating the meadow, its continued existence is evidence that fire does not eradicate the species. Frequently burned tallgrass prairie in Kansas had substantially fewer invasive species than infrequently burned or unburned prairie (Smith & Knapp 2001). These results demonstrate the importance of fire as a maintenance tool in mesic grasslands.

Fire substantially decreased the fraction of total biomass that *Galium* contributed relative to other treatments, however fertilization increased the fraction, indicating that physical disturbance is the mechanism by which fire inhibits *Galium* productivity. In July, the burned plots had higher plant-available soil nitrogen concentrations than ambient conditions. Due to this disturbance, *Galium* was unable to take advantage of the modest post-fire nutrient pulse.

It was surprising that the burned plots had significantly lower C₄ grass biomass than unburned plots. The grasses in my plots responded vigorously, but were not nearly as large as the same species growing in the large, burned xeric section of the Blandy meadow (personal observation). Most studies have found an increase in warm-season grass productivity with fire (e.g., Blair 1997), but there is some evidence for declines in production with burning (Wilson & Shay 1990). Increased productivity can be explained by increased soil temperature and light availability on burned sites (Peet et al. 1975). My small-scale burn may not have produced a large enough gap to substantially increase light

in the canopy or temperature at the soil surface or the intensity of my small-scale fire may have provoked different responses than larger, often less intense prescribed burns or wild fires (Ewing & Engle 1988).

Diversity Effects

The lack of a diversity effect was somewhat surprising. In addition to sheer species richness, functional group richness has also been shown to be an important determinant of invasibility in many communities (Symstad 2000). Several of these studies have focused on functional similarities between abundant native species and invaders. Oftentimes communities are invaded by species from functional groups other than those of the dominant or most abundant species (Pokorny et al. 2005). The tallgrass prairie ecosystem is dominated by graminoids, and this meadow was established without systematic manipulation of herbaceous species diversity or abundance. Despite these findings, different species within a functional group (graminoids, forbs, etc.) may have quite different niches and alter ecosystem functioning to a greater degree than a more functionally diverse community (Wright et al. 2006). There is some evidence that dominant species *A. gerardii* and *S. nutans* are not as similar physiologically or ecologically as once believed (Silletti & Knapp 2001; Silletti et al. 2004).

The diversity effect could be driven by *Andropogon gerardii*, the largest and most dominant species of this community. There is a chance that differences among diversity levels were not evident because the abundance of *Galium* was regulated to a large extent by *A. gerardii*. This species composed the majority of nearly all plots. Although *A. gerardii* biomass varied in individual plots, the effect of *A. gerardii* upon *Galium* may

have saturated. Dominant species can completely drive the community's ability to resist invasion (Emery & Gross 2007), making additional species unnecessary for invasion resistance and confounding diversity-invasibility relationships (Aarssen 1997). Smith et al. (2004) reported a significant effect of *A. gerardii* on exotic species establishment and success. As the dominant species at Blandy, *A. gerardii* could also be responsible for the relationship seen in the current study.

The diversity manipulations in this experiment may provide a more realistic approach to changes in species richness. Species loss from natural communities is non-random, usually caused by biological responses to changing environments (Rinella et al. 2007). As the most dominant grass, *A. gerardii*, presumably will be better able to withstand extreme events (e.g., droughts, fire, disturbance, species invasions) than some of the less abundant species (Blair 1997; Silletti & Knapp 2001, Smith et al. 2004). This change in community composition can be seen as a change based on the biology of individual species. Although *Sorghastrum nutans* is a codominant, it is more similar to *A. gerardii* than *Schizachyrium scoparium*. *S. scoparium* may persist under poor conditions due to its size difference from the dominant tallgrasses and the fact that *S. scoparium* is a bunchgrass. These traits and physiological differences between the species may allow them to coexist through complementarity under adverse conditions (Fargione et al. 2005; Gross et al. 2007).

Nutrient additions affected species similarly at all three diversity levels in this experiment. Species richness had a much weaker effect on the invasibility of this meadow than nutrients or disturbance. This finding may allow managers to focus on ecosystem

characteristics when restoring degraded habitats or devising control strategies for invasive species. It seems that low nutrient environments with high or low species diversity are equally susceptible to invasion by exotic species when excess nutrients are introduced. Current anthropogenic activities have caused worldwide increases in reactive nitrogen concentrations (Galloway et al. 2004) which will likely hasten the spread of exotic species. By taking into account the biology of native and invasive species, appropriate measures can be undertaken to halt the spread of invasive species and restore native habitats.[dci4]

Table 5. Summary of Analysis of Variance results for soil nitrogen. A) Total plant-available nitrogen in July, B) Plant-available nitrate in July, C) Plant-available ammonium in July, D) Plant-available total nitrogen in September, E) Plant-available nitrate in September, F) Plant-available ammonium in September.

	A) Total N - July			B) NO ₃ ⁻ - July			C) NH ₄ ⁺ - July		
	df	F	p	df	F	p	df	F	p
Whole Plot									
Diversity	2	0.92	0.43	2	0.23	0.8	2	1.9	0.21
Error	9	--	--	9	--	--	9	--	--
Sub-plot									
Nutrients	3	31.86	0.001	3	34.72	0.0001	3	5.14	0.006
Diversity*Nutrients	6	0.2	0.97	6	0.38	0.89	6	0.18	0.98
Error	27	--	--	27	--	--	27	--	--
	D) Total N - September			E) NO ₃ ⁻ - September			F) NH ₄ ⁺ - September		
Whole Plot									
Diversity	2	0.6	0.57	2	1.67	0.24	2	7.04	0.01
Error	9	--	--	9	--	--	9	--	--
Sub-plot									
Nutrients	3	54.77	0.0001	3	77.06	0.0001	3	3.63	0.026
Diversity*Nutrients	6	2.57	0.04	6	1.81	0.13	6	0.36	0.9
Error	27	--	--	27	--	--	27	--	--

Table 6. Summary of analysis of variance responses by warm-season grasses. A) Warm-season grass biomass at harvest, B) *Andropogon gerardii* biomass at harvest, C) Total plot biomass (forbs + grasses) at harvest, D) Warm-season grass tiller density in July, E) Warm-season grass tiller density in September.

	A) WSG Biomass			B) <i>A. gerardii</i> Biomass			C) Total Biomass		
	df	F	p	df	F	p	df	F	p
Whole Plot									
Diversity	2	1.15	0.36	2	11.43	0.0034	2	0.49	0.63
Error	9	--	--	9	--	--	9	--	--
Sub-plot									
Nutrients	3	7.32	0.001	3	5.01	0.0069	3	17.1	0.001
Diversity*Nutrients	6	1.19	0.34	6	2.37	0.058	6	0.48	0.82
Error	27	--	--	27	--	--	27	--	--
	D) WSG July Tillers			E) WSG Sept. Tillers					
Whole Plot									
Diversity	2	1.85	0.21	2	5.27	0.031			
Error	9	--	--	9	--	--			
Sub-plot									
Nutrients	3	6.40	0.002	3	9.73	0.0002			
Diversity*Nutrients	6	1.07	0.40	6	1.26	0.31			
Error	27	--	--	27	--	--			

Table 7. Repeated-measures analysis of variance on A) Warm-season grass tiller density measured in July and September, B) *Galium verum* stem density measured in June, July and September.

	A) WSG Tillers			B) <i>Galium</i> stems		
	df	F	p	df	F	p
Whole Plot						
Diversity	2	3.21	0.078	2	0.61	0.56
Error	11.8	--	--	11.7	--	--
Sub-plot						
Nutrients	3	13.51	0.0001	3	5.23	0.0095
Diversity*Nutrients	6	1.95	0.11	6	1.31	0.30
Error	28.8	--	--	17.2	--	--
Time						
Time	1	72.68	0.0001	2	39.16	0.0001
Diversity*Time	2	1.22	0.31	4	3.23	0.023
Nutrients*Time	3	0.71	0.55	6	2.49	0.04
Diversity*Nutrients*Time	6	0.30	0.93	12	1.25	0.29
Error	36	--	--	36	--	--

Table 8. Summary of Analysis of Variance results of *Galium* responses. A) *Galium* above-ground biomass, B) Number of *Galium* plants producing seed, C) Percentage of total plot production made up of *Galium*, D) June *Galium* stem density, E) July *Galium* stem density, F) September *Galium* stem density.

	A) <i>Galium</i> Biomass			B) <i>Galium</i> Seed			C) Percent <i>Galium</i>		
	df	F	p	df	F	p	df	F	p
Whole Plot									
Diversity	2	0.91	0.43	2	1.01	0.40	2	1.16	0.36
Error	9.07	--	--	9.12	--	--	9.08	--	--
Sub-plot									
Nutrients	3	20.54	0.0001	3	27.43	0.0001	3	13.64	0.0001
Diversity*Nutrients	6	0.54	0.78	6	0.7	0.65	6	0.73	0.63
Error	26.1	--	--	25.4	--	--	26.1	--	--
	D) June <i>Galium</i> Stems			E) July <i>Galium</i> Stems			F) Sept. <i>Galium</i> Stems		
Whole Plot									
Diversity	2	0.08	0.92	2	0.78	0.49	2	0.44	0.66
Error	9	--	--	9	--	--	9	--	--
Sub-plot									
Nutrients	3	4.19	0.015	3	11.40	0.0001	3	10.13	0.0001
Diversity*Nutrients	6	1.57	0.19	6	3.21	0.017	6	0.52	0.79
Error	27	--	--	27	--	--	27	--	--

Table 9. Split plot analysis of variance for mean soil moisture content. A) Top 5 cm of soil, B) 5 – 15 cm of soil column. Measures were taken five times and averaged.

	A) Moisture Top 5 cm			B) Moisture 5 – 15 cm		
	df	F	p	df	F	p
Whole Plot						
Diversity	2	1.02	0.37	2	3.49	0.08
Error	9	--	--	9	--	--
Sub-plot						
Nutrients	3	1.05	0.38	3	0.79	0.51
Diversity*Nutrients	6	0.92	0.49	6	0.77	0.60
Error	27	--	--	27	--	--

Chapter 4. *Conclusions*

This thesis examined the effects of nutrient pulses on invasive species in two very different habitats: a deciduous forest understory and a warm-season grassland. There were several noteworthy similarities between these. Differences in the physiology and life history of native species and exotic invaders proved important in both systems. Both studies also lend support to the fluctuating resource hypothesis. Despite the strong effects of nutrient addition, biodiversity-related effects appear to have been unimportant in either system.

Differences between Invaders and Natives

Several important differences between native species and invaders appear to have promoted exotic species success in these dissimilar communities. Wintergreen species such as *A. petiolata* are better able to utilize early nutrient pulses than spring ephemeral species that become active during spring. C_3 forbs, which typically have lower NUE, can invade historically low-nutrient communities dominated by C_4 grasses if those communities become eutrophied. The addition of nutrients alone will not increase the invasibility of every community, as evidenced by invasions in which exotic species have higher NUE than natives (Brewer et al. 2003, Reed et al. 2005). However, nutrient addition aids invasive species in many cases due to differences in physiology or phenology (Allison and Vitousek 2004, Emery 2007). It is not nutrient pulses *per se*, but the manner in which they are utilized that often gives an advantage to non-native species.

Exotic species that possess an important trait (e.g., nitrogen fixation) that all resident species lack, [dcis5]can utilize this novel trait to spread within the community. A.

petiolata possesses such a “triggering attribute” (Gurvich et al. 2005): its early phenology or wintergreen habit. With its ability to grow and utilize nutrients throughout the autumn and winter, *A. petiolata* is able to achieve greater size and fecundity, which may enhance the species’ spread throughout North America.

G. verum does not bring any obviously novel traits to the tallgrass prairie. There are other C₃ forbs in the Blandy grassland, but it is different in many respects from the dominant warm-season grasses. The two most important differences I noted were *Galium*’s earlier phenology and lower NUE than the dominant warm-season grasses. Although I did not include a time component in the nutrient manipulations, the treatments may have been applied early enough to provide *Galium* with an advantage over the native grasses. More importantly, the differences in nutrient-use efficiency among species may provide opportunities for different species to dominate communities with varying resource levels. These differences may have been critical for *Galium* success in fertilized plots. Although plant phenology did not prove very important for success under different soil nitrogen conditions, phenology was likely more important in burned plots. Since burning occurred well after the onset of *Galium* growth, but before the warm-season grasses had grown much, *Galium* was harmed more than were the native grasses. Many studies have shown that early-season fire promotes warm-season grass dominance by releasing nutrients and removing the litter layer before the commencement of native grass growth (Howe 1994, Blair 1997). In addition, early fire harms cool-season species (C₃ species) increasing the advantage of warm-season grasses (Howe 1994, MacDonald et al. 2007).

The combination of nutrient addition with unique invader traits may leave communities susceptible to exotic species invasions. The ability of invasive species to utilize resources that cannot be sequestered by the resident community, due to dormancy or lack of adequate growth rates, provided *Alliaria petiolata* and *Galium verum* with the opportunity to succeed within their new habitats.

Biodiversity and Invasions

Although I examined competitor diversity by different means in each experiment, I found no diversity effects in either community. The removal of *A. petiolata* from a deciduous forest understory did not increase species diversity, nor was competitor diversity correlated with *A. petiolata* adult biomass. I analyzed diversity within the forest understory by making the assumption that *A. petiolata* was responsible for the species diversity present. In the tallgrass prairie system, I examined native species diversity as the causative agent, with *Galium* abundance as a response to native diversity. Similarly, there was no effect of native grass diversity on the success of *Galium*. Although I found no diversity effects, this does not exclude the possibility of these invasive species affecting native diversity or native species diversity having an effect on the success of invaders in this or other systems.

Increasing alteration of natural habitats will continue to promote species invasions. Disturbance and nutrient additions will likely increase the rates at which exotic species colonize some systems. However, these changes alone may not increase the invasibility of ecosystems. Differences between native and exotic species may predispose certain native communities to invasion by exotics under the proper conditions. I have

provided evidence showing that differences between native communities and their dominant invaders can be responsible for the success of these exotic species.

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