EFFECTS OF EXPERIMENTAL INVASIVE COMMUNITIES

ON FOREST DYNAMICS

by

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ABSTRACT OF THE DISSERTATION

Effects of experimental invasive communities on forest dynamics

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Alien invasive plant species have altered the historical descriptions of eastern U.S. forests. This dissertation used an invasive tree (*Acer platanoides*) and shrub species (*Berberis thunbergii*) to examine how experimental understory communities affected dynamics in a suburban deciduous forest in Central New Jersey, USA. With invasive plant removal often an unrealistic option, these community treatments (0%, 25%, 50% invasive) served as proxies for possible management outcomes to test invasive effects on native species.

After only 3 growing seasons, both an *A. platanoides* canopy and *A. platanoides* saplings had strong negative impacts on native sapling and seedling growth. There was such a strong negative effect of the invasive canopy on native sapling growth that the presence of invasive saplings was less important. However, beneath a native canopy, native saplings grew significantly more in the absence of invasive saplings. Even if invasive removal in the understory were only done every 2-3 yrs, this would give native saplings release from invasive competition and time to increase in growth (Chapter 1).

In two separate experiments, an invasive canopy negatively affected native seedling growth in the forest (Chapter 3), and soil collected from beneath an invasive canopy reduced native growth (greenhouse, Chapter 2). While the understory and canopy types impacted native saplings and seedlings, *A. platanoides* was largely unaffected (Chapters 1, 3). However, it does appear that it has the ability to shift

resource allocation depending on soil type, which may give it a growth advantage over native species (Chapter 2). I did not find support of the ERH, as leaves from seedlings of *A. platanoides* and *A. rubrum* had equivalent amounts of herbivory (Chapter 3). In a litter decomposition experiment (Chapter 4), two invasive species had lower C:N ratios than the native species. Higher nitrogen content in invasive litter could alter soil nutrients and cycling and, perhaps, leave a legacy of invasive impact.

Experimental studies done in the field can help us increase our understanding of invasive and native species interactions, while providing us with information to guide restoration and management decisions to retain native diversity.

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I really appreciated the help and guidance of Nicoletta Graf and Gail Johnson in the Rutgers Horticultural Greenhouses; they were invaluable during the greenhouse experiment. I am grateful to Joan G. Ehrenfeld for the use of her lab, which allowed me to do the majority of the litter analysis in Chapter 4. Her graduate students were very helpful and patient while answering my many questions and I thank them all: Kristen Ross, Kenneth Elgersma, Jodi Messina, Emilie Stander, Shen Yu, and Monica Palta.

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Please note that Chapter 1, "Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities", is In Press in *Journal of Ecology*.

DEDICATION

This dissertation is dedicated to

my husband, Dan Kent,

my parents, Jim and Glenna Galbraith,

my grandfathers, Robert Zimmerman and Charles Galbraith,

my grandmothers, Catherine Zimmerman and Ethel Galbraith,

and to all of the other women before me

who would have been good ecologists,

but just didn't have the same opportunities I've had…

I hope to make you proud.

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log$_{10}$ – transformed to increase normality. The predictor variables were either log$_{10}$ or arc-sine transformed. The analyses were done for seedlings of both species, *Acer platanoides* and *A. rubrum*.

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as light bars, while communities with invasive saplings (25% and 50%

invasive) are represented as dark bars (see Table 1 for community

planting design). The invasive canopy dominant species was *Acer*

platanoides, while several native species were canopy dominants, depending

on the plot [including *A. rubrum, Fraxinus americana, Quercus alba, Q.*

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Mean values ± 1 SE, level of significance, and the number of saplings per

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2006 September). Communities with *A. platanoides* comprising 25% of

the saplings are shown as dashed horizontal bars, while communities

with 50% of the saplings being *A. platanoides* are represented with

vertical striped bars (see Table 1 for community planting design). The

invasive canopy dominant species was *Acer platanoides,* while several

native species were canopy dominants, depending on the plot [including

A. rubrum, Fraxinus americana, Quercus alba, Q. palustris, and

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INTRODUCTION

Just as Jared Diamond (Diamond, 1999) discussed the characteristics and fates of cultures through time, the causes and consequences of exotic species proliferation are ideas the field of ecology is trying to understand and describe (Mack *et al.*, 2000; Rejmanek & Richardson, 1996; Williamson & Fritter, 1996). Beginning in the 1800s with Charles Darwin and Alfred Russel Wallace, through the foundational writing on exotic invasive species by Charles Elton (Elton, 1958), how and why species are distributed the way they are have been important components of ecology. With increasing globalization and human interactions, species continue to be dispersed to newer regions. As a result, most ecologists are finding that exotic invasive species (hereafter, invasive) are having negative effects on native species diversity and functioning within diverse ecosystems. However, these issues of conservation and natural resource management are challenged by some who believe the field of invasion ecology is flawed socially, as described by Dan Simberloff (Simberloff, 2003), or lacking in objective scientific rigor (Theodoropoulos, 2003). For these reasons and more, research in invasive ecology is relatively new and in need of more experimental study.

Some of the studies common in invasive research have addressed community assembly (Tilman, 2004; Young *et al.*, 2001) and diversity-invasion questions (Kennedy *et al.*, 2002; Naeem *et al.*, 2000; Stohlgren *et al.*, 2003; Stohlgren *et al.*, 1999), which may have as much fervor as the disagreements between Gleason's species concept (Gleason, 1926) and Clements' forest climax (Clements, 1936) during the early 20th century. However, in the discussion of native diversity and species invasion, a key concept to address is what exactly is "natural" (McNeely, 2000), since many of our communities have become mixtures of native, naturalized, and invasive species

(Bridgewater, 1990; D'Antonio & Meyerson, 2002) through human disturbance and introductions over the past four centuries.

In this dissertation, I experimentally evaluated the effects of different invasive sapling densities in forest understory communities. By setting the community structure through the establishment of sapling plot treatments, monitoring the growth and characteristics of those communities, and by looking for structural (*e.g.,* species growth patterns) and functional differences (*e.g.,* herbivory, soil dynamics) among the communities, I have followed a process similar to what Margaret Palmer and colleagues (Palmer *et al.*, 1997) have suggested for ecological restoration (Fig. 1). They recommended doing restoration within a community ecology framework and as a sequential, multi-step process: (1) restore desired species richness (*e.g.,* community structure), (2) monitor the development of the community, and (3) verify linkages between community structure and function have been established.

While many studies call for invasive research to be done on relatively large scales (Mack *et al.*, 2000; Parker *et al.*, 1999; Stohlgren *et al.*, 1999), which includes more complex effects including dispersal and disturbance, land managers at local scales are in desperate need of answers concerning invasive plants (Clewell & Rieger, 1997; Young *et al.*, 2005). To my knowledge, this study is the first to use experimental communities with woody species that were planted at proportions to mimic three management outcomes.

One of the two invasive species I used in this study was *Acer platanoides* L. (Norway maple), which is a shade-tolerant invasive tree species introduced in the eastern United States of America (US) during the mid-1700s (Nowak & Rowntree, 1990). Other than a study identifying its presence in the Hutcheson Memorial Forest in Somerset, NJ (US) (Monk, 1961) and another in the 1970s which found some anti-fungal properties in its leaves (Dix, 1974), the first study describing the invasion pattern, and

possible consequences, of *A. platanoides* into deciduous forests was done by Sara Webb and Christina Kaunzinger (Webb & Kaunzinger, 1993). The work by Webb and her students at Drew University in Madison, NJ (US) (Webb *et al.*, 2000; Webb *et al.*, 2001; Wyckoff & Webb, 1996) has shown that *A. platanoides* canopies facilitate growth of conspecific seedlings, inhibits native regeneration and diversity, and, that, while removal of *A. platanoides* seedlings may increase native seedling abundance, individuals of other invasive species also increase. At the same time, Patrick Martin did a study in upstate New York (US), in which he supported Webb and Kaunzinger's early study and quantified seedling and sapling reductions of *A. saccharum* Marsh. beneath *A. platanoides* adult trees (Martin, 1999).

Though most of the work on *A. platanoides* in our country has been done in the eastern area (Anderson, 1999; Bertin *et al.*, 2005; Cincotta, 2006; Fang, 2003; Hunter & Mattice, 2002; Kloeppel & Abrams, 1995; Martin & Marks, 2006; Morrison & Mauck, 2007; Rich, 2004; Sanford *et al.*, 2003), this species has also been identified as invasive in Midwestern (Wangen *et al.*, 2006; Webster *et al.*, 2005) and western forests (Reinhart *et al.*, 2005). Using a system in the Rocky Mountain region, Kurt Reinhart has increased our understanding of conspecific facilitation by *A. platanoides* (Reinhart *et al.*, 2006a), through mechanisms associated with increased shade and soil moisture in forests (Reinhart *et al.*, 2006b) and release from natural biotic enemies in the non-native soil (Reinhart & Callaway, 2004).

Two recent dissertations using *A. platanoides* as their study species were done in the same region as my study (eastern U.S.) (Fang, 2003; Rich, 2004). It had been suggested earlier that allelopathy might be a mechanism supporting the success of this invasive (Sauer, 1998; Wyckoff & Webb, 1996) and Betsy Rich (Rich, 2004) tested this hypothesis in the forest and greenhouse, but found if *A. platanoides* does have any allelopathic properties, they are minimal at best.

In Long Island, NY (US), Wei Fang evaluated the spatial effects of an *A. platanoides* invasion and the impacts of existing canopy adults on functional communities and ecosystem dynamics, using *A. rubrum* as the native congener (Fang, 2003). In my dissertation, I also used those two species, because *A. rubrum* L. was more important than *A. saccharum* at my study site (Galbraith-Kent, Chapter 1), it has a large ecological amplitude (Harlow *et al.*, 1996; Walters & Yawney, 1990), is increasing in eastern forests (Abrams, 1998; Galbraith & Martin, 2005), and because of these reasons, I believe it might be a good species choice for restoration in forests disturbed by invasions. While Fang used existing canopies to test understory effects, my study evaluated how experimental understory communities (tree and shrub communities), including species in addition to *A. platanoides* and *A. rubrum*, affected forest dynamics.

The other invasive species used in this dissertation was *Berberis thunbergii* DC, a shrub native to Japan (Ohwi, 1965). In understories of eastern U.S. forests, *B. thunbergii* can form dense, monospecific stands (Cassidy *et al.*, 2004; Ehrenfeld, 1999; Hunter & Mattice, 2002; Lundgren *et al.*, 2004; Silander & Klepeis, 1999). Joan G. Ehrenfeld and her colleagues have found *B. thunbergii* to alter soil functioning (Kourtev *et al.*, 1998) and increase nitrification, which is likely a positive feedback contributing to its success and persistence (Ehrenfeld *et al.*, 2001), perhaps at the detriment of native shrubs. Due to its abundance at my study site and within the region, *B. thunbergii* was chosen as the invasive shrub in the experimental communities.

The main question I had that was driving the direction of this dissertation was, *"What happens if invasive woody saplings cannot be completely removed from the understory of a deciduous forest?"* To test this, there were four related experiments evaluating the dynamics of woody species at multiple forest strata (*i.e.,* canopy, sapling, seedling, litter) (Fig. 1). All four data chapters were written and prepared as manuscripts for submission to specific journals. While this is my personal dissertation, the majority of

the writing is in 1st person plural using the "we" pronoun, since the manuscripts will be

submitted with my dissertation director (Steven N. Handel) as the co-author. Chapter

submissions to journals will likely be:

- Chapter 1 – Journal of Ecology (*Accepted*, *In Press*) – Invasive *Acer platanoides* inhibits native sapling growth in understorey forest communities.

- Chapter 2 – Canadian Journal of Botany – Interactions between the invasive *Acer platanoides* (Norway maple) and native *Acer rubrum* (red maple): effects of interspecific competition and soil type on seedling growth.

- Chapter 3 – American Journal of Botany – Growth and herbivory of *Acer* seedlings in the understory of a mixed hardwood forest: comparison between an invasive and native species.

- Chapter 4 – Journal of the Torrey Botanical Society – Litter decomposition dynamics of invasive and native species within experimental forest understory communities.

The *first* experiment (Chapter 1) was established in a forest understory by

transplanting invasive and native saplings (0.25 – 1.0 m height) into experimental

communities (4m x 4m plots, each containing 36 plants) differing in proportions of

invasive plants (0%, 25%, 50% invasive). These tree and shrub community treatments

were chosen as the native control (0% invasive), as the treatment containing the same

number of plants per species, including invasive (25% invasive) (*i.e.,* 9 plants per

species), and the treatment where the plant number of the invasive species equaled the

total number of all native plants (50% invasive). These treatments served as proxies for

possible invasive management outcomes in a forest understory. To give inferences on

future canopy composition through competitive interactions, performance (growth and

survival) of native species was compared to the invasives over a 3-yr growing period. At

this time, the shrub saplings have not shown particularly clear trends; so, only the tree

communities have been discussed. The main hypotheses tested were:

1. *A. platanoides* saplings would negatively impact native plant growth, so that the native tree saplings would perform best in community plots where invasive plants were absent (*i.e.*, 0% invasive community).

2. Native saplings would grow best underneath a native canopy, rather than an invasive canopy (*i.e., A. platanoides*).

Due to their genetic similarities, using congeneric pairs to test interactions between native and non-native invasive species has been identified as an important method for recognizing traits that may give invasives competitive advantages (Mack, 1996). After seeing some initial trends in species responses within the experimental forest communities, the *second* experiment (Chapter 2) was undertaken. To better understand the interactions of the invasive *A. platanoides* with its congener, *A. rubrum*, this experiment was done in a greenhouse to evaluate the impacts of soil [collected from beneath two canopy types: invaded (*A. platanoides*) and native (several species)] and inter- and intraspecific competition on seedling growth. Based on other studies that showed facilitation (Reinhart *et al.*, 2006a; Wyckoff & Webb, 1996) and covered species ecology (Meiners, 2005), these hypotheses included:

1. *A. rubrum* would grow better in native forest soil, while *A. platanoides* would have greater growth in invaded forest soil.

2. *A. platanoides* would have greater overall growth than *A. rubrum* and both species would grow better with a conspecific seedling when competing above- and below-ground.

Serving as a field complement to the greenhouse study, the *third* experiment (Chapter 3) evaluated *Acer* seedling growth beneath the tree and shrub sapling communities established in the forest in the first experiment. Seedlings were planted as pairs with conspecifics and heterospecifics to test the effect of neighbor identity on growth over a 1-yr period. In addition, the enemy release hypothesis (Wolfe, 2002) was tested by analyzing foliar herbivory of the two species. Hypotheses tested included:

1. *A. rubrum* seedlings would grow better (a) beneath communities lacking invasives and (b) with a conspecific seedling neighbor, rather than an *A. platanoides* neighbor.

2. Using digital leaf area analysis, *A. rubrum* would have a greater amount of foliar herbivory than *A. platanoides*.

Within those same sapling communities, the *fourth* experiment (Chapter 4) evaluated the litter decomposition and chemical characteristics of two invasive and two native plant species (Ashton *et al.*, 2005; Ehrenfeld, 2003). Litter bags containing monospecific litter were evaluated for mass loss and C:N ratio at four times over a 1-yr period at 4 wks, 20 wks, 40 wks, and 53 wks. Based on the main question of the dissertation, I wanted to know if understory communities containing invasive plants had an impact on soil functioning after 2 yrs of establishment. The hypotheses tested were:

1. After being established for 2 yrs, understory communities containing invasive saplings would have developed different soil properties (*e.g.,* greater nitrogen, higher pH), faster litter decomposition rates and lower C:N ratios than purely native communities.

2. Litter of invasive species (*i.e., A. platanoides, B. thunbergii*) would decompose faster and have lower C:N ratios than the native species (*i.e., A. rubrum, V. dentatum*).

Few studies have tested at the community level the impact that invasive species are having on native plants in forests. Many descriptive studies have shown the negative effects of invasive species on native plant abundance and richness, but relatively few have tested these observations in an experimental setting in a forest. It is a safe assumption that most invasive species will not be removed from forests, due to various financial and logistical constraints, so this study was done to find out what happens when that occurs at various proportions. Understanding how native andi nvasive plant species respond under these realistic outcomes can offer us insight into our future forests.

CANOPY TREES

Ch. 1, 3, Overstory canopy effects

SAPLING COMMUNITIES

Ch. 1, Interspecific competition

Ch. 2, Interspecific competition & soil effects

SEEDLINGS

Ch. 3, Interspecific competition & herbivory

SOIL

Ch. 4, Litter decomposition
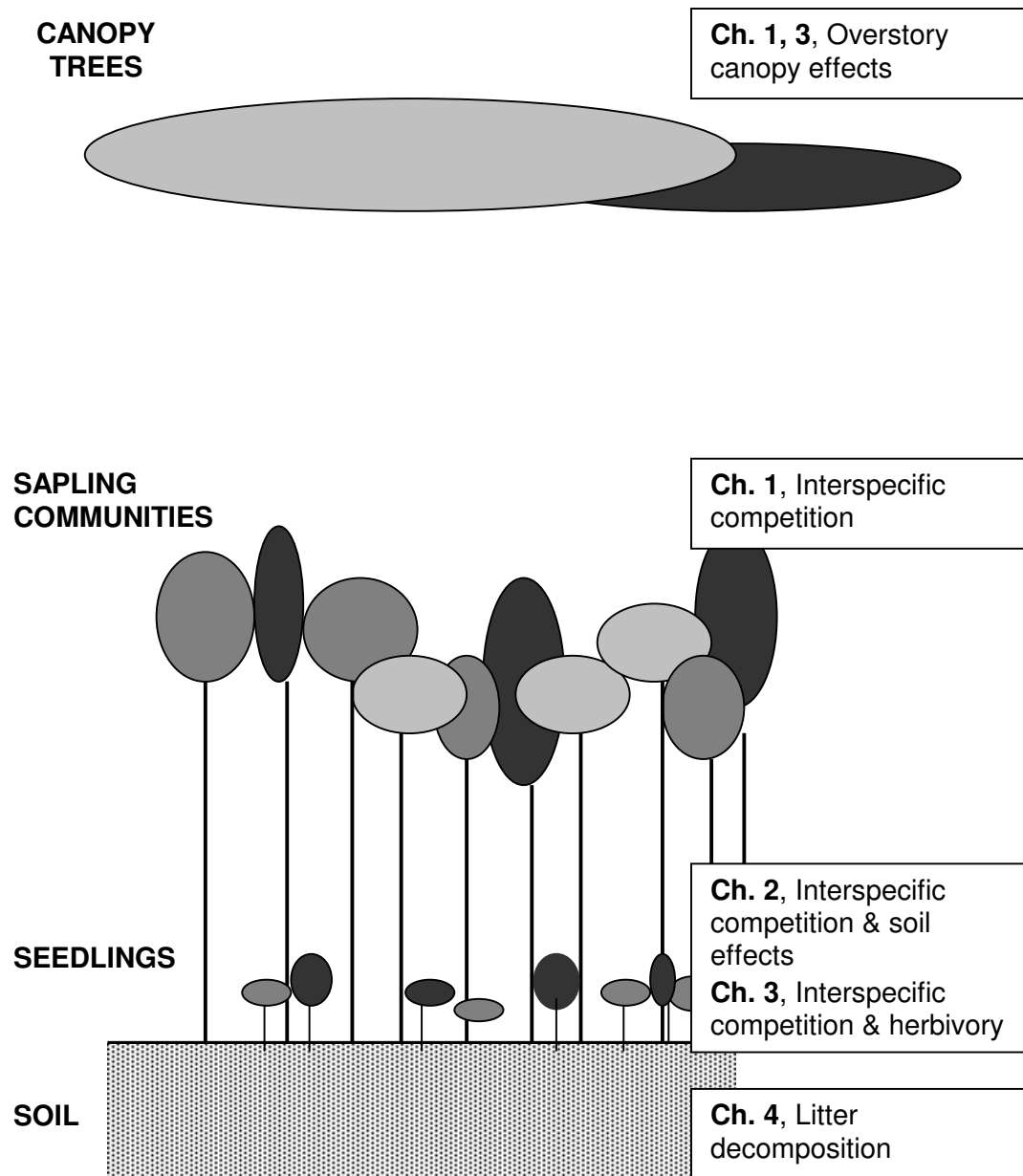
Figure 1. The organization of the dissertation chapters by overstory canopy, sapling, seedling, and soil layers of a deciduous forest in central New Jersey, USA.

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CHAPTER 1

Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities

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SUMMARY

1. Over 3 growing seasons, we tested how an invasive tree species (*Acer platanoides*) affected native plant growth in understorey communities of a suburban forest in central New Jersey, USA. We planted similar aged and sized saplings ($\geq$ 0.25 m tall) into experimental plots identified with one of three treatments (0%, 25%, and 50% of total stems are invasive species) and hypothesized native species would grow better in communities lacking invasive plants.

2. There was a plant survival rate of 90% for the duration of the experiment, but in treatments where natives competed with *A. platanoides*, growth of native species was significantly less than in the purely native stand. In 2006, the mean height of *A. rubrum* was 110 cm ($\pm$ 4 SE) in communities with the highest proportion of *A. platanoides*, while it was 149 cm ($\pm$ 7 SE) in the 0% invasive communities. Conversely, *A. platanoides* grew similarly in treatments where it comprised two different proportions and beneath both canopy types (*i.e.,* invasive and native).

3. Native saplings were 28% shorter beneath an invasive canopy (*i.e., A. platanoides*), compared to a native canopy. An interesting interaction existed between community treatment and canopy type, as the invasive canopy had such a strong negative effect on native growth that the presence of invasive saplings was irrelevant. However, beneath a native canopy, the absence of

invasive saplings significantly increased growth of native saplings. Since the extent and rate of invasive proliferation often makes complete removal unrealistic, this study supports episodic removal (every 2-3 yrs) of this invasive sapling.

4. Synthesis: This experiment showed that native sapling growth was inhibited (1) when growing beneath an invasive canopy and (2) when competing with *A. platanoides* in forest understorey communities. It appears canopy type is more important, because the negative effects from an invasive canopy were strong enough that the co-occurrence of invasive saplings had no impact on native growth. The capability of *A. platanoides* to inhibit native saplings through understorey competition and overstorey canopy effects, while not affecting conspecifics, may contribute to its success as an invader of North American forests.

KEYWORDS

Acer platanoides, Acer rubrum, forest canopy, forest understorey communities, interspecific competition, invasive species, Norway maple, *Quercus rubra*, *Ulmus americana*

INTRODUCTION

Non-native, exotic plant species that become invasive continue to impact ecological structure and function (Fox & Fox, 1986; Luken & Thieret, 1997; Mooney & Drake, 1986; Mooney & Hobbs, 2000). These species are often named as the cause for declines in native biodiversity (McKinney & Lockwood, 1999; Wilcove *et al.*, 1998) and can complicate ecological restoration efforts (D'Antonio & Meyerson, 2002).

A key concept to address in the greater discussion of invasion and species diversity is, "what exactly is natural?" (McNeely, 2000), since many of our communities have become mixtures of native, naturalized, and invasive species (Bridgewater, 1990; D'Antonio & Meyerson, 2002) through human disturbance and introductions over the past four centuries. While it is generally desirable to remove invasive plants through a variety of methods (*e.g.,* by hand, mechanically, fire), removal may actually increase subsequent invasions (Luken, 1997; Webb *et al.*, 2001) or destabilize the soil (Wootton *et al.*, 2005) or be economically impossible (Ewel & Putz, 2004). In many cases, the most realistic option is not full eradication of the invasive plants (Alvarez & Cushman, 2002; Daehler, 2003; Sauer, 1998), but making the "most out of a bad situation" while retaining some of the invasives (D'Antonio & Meyerson, 2002).

With this reality in mind, understanding how native plant communities are affected by invasive species is of interest. Many invasive plants have been shown to decrease species richness (Collier *et al.*, 2002; Martin, 1999) and may replace native species as the compositions of natural communities become more homogenized (McKinney & Lockwood, 1999), possibly affecting the ability of our forests to provide ecological services (Webster *et al.*, 2006). The majority of North American studies documenting effects of invasive woody species in forests, such as *Rhamnus spp.* (Fagan & Peart, 2004; Knight & Reich, 2005), *Acer platanoides* (Martin, 1999; Reinhart *et al.*, 2005; Webster *et al.*, 2005) and *Berberis thunbergii* (Cassidy *et al.*, 2004) have all

used naturally occurring trees and shrubs, or a design similar to a common garden experiment (Sanford *et al.*, 2003).

We used an experimental study in a forest to test how *Acer platanoides* L. (Norway maple) affected the growth of co-occurring planted native tree saplings in understorey communities. *A. platanoides* is a European invasive tree species that was intentionally introduced in North America in 1756 (Nowak & Rowntree, 1990), and has continued to spread in eastern (Martin, 1999; Webb *et al.*, 2000), midwestern (Wangen *et al.*, 2006), and western (Reinhart *et al.*, 2005) North American forests. The high growth rate (Kloeppel & Abrams, 1995), recruitment and persistence of *A. platanoides* in open and closed forests is typically much greater than native trees, which causes concern for the structure and functioning of future forests (Martin, 1999; Sanford *et al.*, 2003; Wyckoff & Webb, 1996).

A recent review found that more than 90% of the studies testing the effects of invasive plants on native community structure were observational, while nearly all experimental studies investigating effects of invasives on native plants used just one native species (Levine *et al.*, 2003). To our knowledge, this temporal study is one of the first to experimentally test the growth of invasive and native saplings in forest understorey communities. We sought to test how varying proportions of a common invasive plant affected the growth and survival of several co-occurring native species. By using these treatments, we tested if there was a population threshold where invasives reduced native sapling growth. We planted all species simultaneously and at the same life-stage to minimize priority effects, which can alter outcomes of species interactions in experiments (Morin, 1999), and assembly differences, since late-arriving species may only establish if necessary resources are not consumed by species already present (Tilman, 2004).

In this experimental study, we tested how different abundances of an invasive plant affected native species performance (as measured through height, volume, and mortality) over 3 growing seasons. We hypothesized that *A. platanoides* would reduce native plant growth, so that the native trees (*Acer rubrum* L., *Quercus rubra* L., *Ulmus americana* L.) would perform best in treatments where invasive plants were absent.

METHODS

This field study evaluated the effect of local invasive sapling (*A. platanoides*) abundance on the survival and growth of native tree saplings in a forest understorey. All saplings (native and invasive) were planted at the same time for this experimental design.

Study site

We conducted this study in a post-agricultural secondary forest in the Piedmont of central New Jersey (Somerset County, NJ) on the property of Duke Farms (1093 ha total) (N 40˚33.8´ W 74˚25.4´). This forest (0.36 ha = 3600 m^2) had an overstory canopy (stems > 2.5 cm dbh) dominated by native trees similar to historic descriptions of mixed oak forests in the area (Braun, 1950; Collins & Anderson, 1994; Monk, 1961): *Quercus alba* L. (relative IV=19.2%), *A. rubrum* (relative IV=16.9%), *Q. palustris* Muenchh. (relative IV=14.5%), and *A. platanoides* (relative IV=11.9%) (S. Galbraith-Kent, *unpublished data*). The understorey was primarily composed of defined patches of the annual invasive grass, *Microstegium vimineum* Trin. Camus and *B. thunbergii*. The soils in the forest are deep (< 200 cm to fragipan), loamy, and the primary type is Dunellen sandy loam (3 to 8% slopes), with secondary types of Lamington silt and Penn silt loam (0 to 2%, 2 to 6% slopes, respectively) (NRCS, 2007).

Between 1971 and 2000, annual mean precipitation for this region of the state has been 126.5 cm, with a mean annual temperature of 10.5°C. During the data collection years of this experiment (2004, 2005, and 2006), precipitation and temperature values were above normal. Illustrating the recent climate variability, the combined months of August and September 2005 had been the warmest and driest on record, while October 2005 was one of the region's wettest months (ONJSC, 2007).

Design of experiment

A replacement series experiment using tree community plots was planted in a randomized complete block design to test the effect of varying invasive proportion (0%, 25%, and 50% plot treatments) on native and invasive species growth and survival. Three main fixed effects (Time, Treatment, Species) were tested across four sample periods and various plot characteristics were measured to explain species growth patterns over time.

Plot location and construction. In June 2004, locations were selected for 15 experimental woody community plots in the secondary forest at Duke Farms. This forest was part of a 14 ha area that was enclosed by a deer fence, preventing large mammal herbivory. Plots were placed in areas that did not contain *B. thunbergii* and were not in low-lying moist depressions. The absence of *B. thunbergii* was important, so that all plots were initiated in soil chemistry conditions not directly affected by this invasive (Ehrenfeld *et al.*, 2001). However, the majority of plots had 100% cover of *M. vimineum*, differing only in density of the grass; these conditions were noted per plot at time of grass removal. All of the grass was removed by hand, with the leaf litter and woody debris remaining.

In July and August 2004, 15 tree community plots were designated, with five plots per treatment type: 0% of the plants are invasive species (*i.e.,* 100% native), 25%

invasive, and 50% invasive. Plots were assigned treatment types using a randomized

complete block design, which helped spatially balance all three treatments across the

forest and control for unwanted variation (Potvin, 2001). In each of the five spatial

blocks in the forest, one plot of each tree treatment was present. We used a deWit

replacement series design and kept the plant density per plot (n=36 plants / plot) the

same, but varied the number of plants per species (Table 1). The density of stems was

chosen in response to plant sizes and the experimental constraints of logistics and

scale. All plots (4 m x 4 m) were separated by at least 2 m and planted with the same

spatial pattern of six plants per six rows with equal plant spacing (0.5 m). Across all

plots, there were a total of 540 tree saplings and an equal number of plants per species

(n=180) (Table 1). Based on initial sapling sizes in 2004, the plot size and density were

chosen to encourage plant interactions from the beginning of the experiment. When a

plant died, it was replaced in October or the following April with a living plant new to the

plot. This re-planting allowed the species proportions of treatments to remain consistent

through the duration of the experiment.

As stated above, the summer of 2005 set records for high temperatures and a

lack of rain. To keep the plants alive during this time, we added 18.5 to 30 litres of water

to each plot 4-5 times per week. For any given week, all 15 plots received the same

amount of water to maintain consistency.

Species selection. All native plants selected were regional genotypes that had

historical (Collins & Anderson, 1994; Monk, 1961) or current presence in the area

(Handel & Clements, 2003) and were donated from Greenbelt Native Plant Nursery

(Staten Island, NY). Each tree community plot contained three native species (*A.

rubrum*, *Q. rubra*, *Ulmus americana*), with proportions depending on treatment type.

At the study site in 2004, *A. platanoides* was common as a seedling and

overstorey canopy tree, but not abundant in the sapling size-class. Therefore, we used

saplings transplanted from two sites (Wissahickon Watershed, Philadelphia, PA; Drew University, Madison, NJ), which were then placed into the 25% and 50% invasive tree plots. We chose saplings that were between 0.25 and 0.75 m tall, so that all plants (invasive and native) were mature understorey saplings of similar size and age at the time of planting.

Plot characteristics

The understorey light environment for each plot was measured using digital photographs from a 36-mm Canon PowerShot S410 Digital Elph (4.0 megapixels) (Canon Corporation, Japan). This indirect measure was previously described (Ashton *et al.*, 2005; Engelbrecht & Herz, 2001) as a good estimate of light when compared to more direct measurements (*e.g.,* Leaf Area Index). On August 23, 2006 (at noon during partly overcast conditions), we took a photograph in the center of each plot, where the camera was leveled on a small tripod 1.5 m from the ground surface. Photographs were taken with the camera lens facing up toward the canopy and the top of the camera (containing the shutter button) facing magnetic north. For all photos, the lens was at a constant aperture (f = 2.8) and zoom and flash were disabled. The amount of open sky in the field of vision was determined using Adobe Photoshop 5.5 (Adobe Systems, San Jose, CA, USA) as previously described (Ashton *et al.*, 2005; Engelbrecht & Herz, 2001).

Additionally, for each of the 15 plots, the existing dominant canopy tree species and percentage of its total cover was observed. We also measured the distance to the nearest shrub species (NSS), NSS volume, distance to nearest tree species (NTS), and NTS dbh for each plot. Soil was collected (0-10 cm depth) from each plot on June 19 (2006). Five cores were taken from each plot and combined into one sample for testing. Our samples were analyzed for chemical and textural characteristics by the Rutgers Soil Testing Laboratory (Middlesex County, New Jersey).

Plant data collection

In September 2004 and 2005, June 2006, and September 2006, we measured height, widest width (diameter1), and 90-degrees across widest width (diameter2) on each plant. Since these plots will continue to be monitored for several more years, we did not destructively sample the saplings to find biomass. Instead, we approximated whole plant volume by using the geometric shape [right circular cone (cm^3) = 1/3 * pi * height * radius1 * radius2] that best fit the plant form of each species.

Data analysis

We evaluated the main effects of plot Treatment type, Species, Time, and Canopy dominant on species growth (mean height and volume) across four sampling periods in the years 2004 (September), 2005 (September), and 2006 (June and September). The data were log_{10}-transformed to increase normality (Underwood, 1997) before we did a Repeated Measures multivariate analysis of variance (MANOVA), which used the four samples as the dependent variables [PROC GLM (General Linear Model Procedure), Pillai's Trace tests]. In the overall Repeated Measures MANOVA, we tested for effects on only the native species to maintain equal sample sizes among all treatments, as the invasive saplings were absent in one of the three treatments (*i.e.,* 0% invasive). For each individual species, we did a Repeated Measures MANOVA to test growth differences across time. Tukey's multiple comparison tests using Least Squares Means (PDIFF and LSMEANS options) were done to determine differences among samples when a significant trend was detected. Analyses for height and volume were done separately.

Instead of using PROC MIXED (which some current Repeated Measures studies use), we used PROC GLM for the Repeated Measures MANOVA with individuals that survived the duration of the experiment (n=486 total saplings, n=363 total native

saplings; 90% of original saplings survived); this eliminated inclusion of missing values. The majority of measurements in our study were taken at evenly spaced intervals (*i.e.*, annually in September), which helped meet the assumption of sphericity of equal covariances between sample times for repeated measures (Gotelli & Ellison, 2004). In our mixed effects analysis, we had three independent variables that were fixed effects (Time, Species, Treatment) and one that was random (Canopy dominant and its interactions), which was identified with a RANDOM statement in the PROC GLM program. Two canopy dominant groups (invasive or native canopy) were identified based on the presence or absence of *A. platanoides* as the dominant canopy species above each plot. *A. platanoides* has been shown to drive canopy changes and subsequent reductions in understorey light, which have negatively affected native species (Reinhart *et al.*, 2006b), so we evaluated its canopy impact on our sapling communities. After a significant interaction (Treatment * Canopy dominant) was found in the overall MANOVA, we sorted the data by canopy dominant and sapling community type to better identify these trends through analyses of variance (ANOVA). In a separate ANOVA, we tested the effect of Canopy dominant on the percentage of light at the sapling level of each plot. To maintain normality (Shapiro Wilks $P > 0.05$) and homoscedascity, these data were log_{10} - transformed.

Pearson's chi-square and Fisher's exact test (PROC FREQ), with adjusted alpha levels of $P < 0.0125$ to decrease the Type I error rate, were used to examine the differences between survival and mortality of all the original plants (n=540) among the tree communities.

Using simple linear regressions (PROC REG), we tested the ability of various plot characteristics (light, soil, biotic, and pre-existing conditions) to predict the mean plot plant height in September 2006 (response variable). To increase normality, both response and predictor variables were either log_{10} or arc-sine transformed.

All mean and standard error values in tables and figures are original (non-transformed) values. All analyses were done with SAS version 9.1 for Windows (SAS Institute, Cary, NC, USA).

RESULTS

We found that the heights and volumes of all native species in the tree communities differed over the sampling Time (from 2004 to 2006), by Treatment type, Species, and Canopy dominant (Table 2). The three significant two-way interactions with Time (Time*Treatment, Time*Species, Time*Canopy dominant) indicated the expected temporal variation of plant growth by each species, treatment, and canopy type.

By the last sample period, native plants in communities without *A. platanoides* (*i.e.,* 0% invasive treatment) had significantly greater height and volume than in both treatments where *A. platanoides* was present (Table 3). For example, native saplings were 22% taller and had 40% greater total plant volume in the purely native community (0% invasive) compared to the most invaded community (Table 3). Of the four tree species, heights of *A. rubrum* and *U. americana* were affected by plot Treatment, as both grew significantly better in the 0% invasive treatment than in either of the treatments containing the invasive (*i.e.,* 25%, 50%) (Fig. 1b, 1d). *A. rubrum* saplings had 26% greater height in the 0% community compared to the 50% community (Fig. 1b), while *A. platanoides* had equivalent heights in both treatments where it was present (Fig. 1a). In addition to the effect of Treatment on native species growth, the type of Canopy dominant (invasive or native canopy) was also important (Table 2). Grouped together, saplings of the three native species grew 28% taller beneath a native canopy than an

invasive, while *A. platanoides* showed no growth difference between canopy types (Fig. 2). While the biotic patterns beneath the canopies were significant, we found the percentages of light in plots beneath the invasive (11.4 $\pm$ 1.0%, n=6) and native canopy (10.2 $\pm$ 0.8%, n=24) did not differ ($F_{1, 28}$ = 1.05, *P* = 0.31).

The only significant interaction in the overall MANOVA, other than the expected two-way interactions with Time, was between Treatment and Canopy dominant (Table 2). This was interesting, as *A. rubrum* and the grouped native species had different growth trends in the sapling community treatments depending on the canopy type (Fig. 3). Beneath an invasive canopy, we found that the type of understory community does not affect native sapling growth, as plants grew similarly in the native (0%) and invasive (25% and 50%) communities. However, when *A. rubrum* saplings grew under a native canopy, they were significantly taller (23%) in the native communities than in the invasive communities (25% and 50% communities) ($F_{1, 69}$ = 13.14, *P* = 0.0005) (Fig. 3). Overall, it appears that an invasive canopy has such a strong negative effect on native sapling growth that the presence of invasive saplings is irrelevant, while the absence of invasive saplings beneath a native canopy significantly increases native plant growth. Though native species showed a significant interaction between Treatment and Canopy dominant, *A. platanoides* had similar growth patterns in sapling communities beneath each canopy (Fig. 4).

We also found many plot characteristics significantly predicted mean native plant height (Table 4), but most of these relationships were not very strong, as the highest R-squared (R^2) value was 0.12 (negative effect of leaf litter depth on sapling height). Other variables (*i.e.,* Treatment, Canopy dominant) likely had greater predictive value for sapling height. However, we did find positive growth when incoming light was high, when existing shrubs and trees were closer to the plot, leaf litter depth was shallow, and the soil had higher concentrations of nitrogenous compounds.

Of the original 540 saplings planted in 2004, 90% survived the duration of the experiment. Compared to treatments where invasive plants were present at proportions of 25% (84% survival) and 50% (83% survival), there was a significantly greater survival of native trees in purely native communities (97% survival) (Pearson's chi-square = 17.33, df = 2, P = 0.0002).

DISCUSSION

The impact of non-native invasive species on natural systems continues to be shown through studies investigating interspecific competition (Hamilton *et al.*, 1999) and alterations of native plant communities (Martin, 1999; Von Holle *et al.*, 2003; Wyckoff & Webb, 1996) at multiple scales (Pauchard & Shea, 2006). In the eastern US, the majority of forest studies evaluating invasive impacts have been observational (Martin, 1999; Webb *et al.*, 2000), or experiments with species removals (Gould & Gorchov, 2000; Luken & Shea, 2000; Webb *et al.*, 2001), or additions focusing on a target invasive species (Gorchov & Trisel, 2003). Our study was one of the first to test the effects of invasive woody species, at varying proportions, on native tree saplings in experimental forest understorey communities.

We found that there were significant effects of all four main factors (Time, Treatment, Species, and Canopy dominant) on heights and volumes of native saplings over the 3 growing seasons. Due to different life histories of the three species (from three genera), we expected that sapling growth per species would differ. Additionally, temporal variation for each of the main effects was confirmed through the three significant two-way interactions with Time (*e.g.,* Time*Species). All three native species had greater survival and growth in plots where the invasive *Acer platanoides* was absent

(0% invasive) (Table 1), compared to plots with 25% and 50% of the invasive. The lack of a Treatment*Species interaction effect on both mean height and volume suggests that each native species responded similarly between the treatments of varying invasive proportions.

When *A. rubrum* was growing with *A. platanoides* saplings, its height was significantly less than when the invasive was not present. In the last survey period, *A. rubrum* saplings in the purely native communities (0% invasive) were 16% and 26% taller than *A. rubrum* saplings in plots containing *A. platanoides* at 25% and 50% proportions, respectively. It also appears that *A. rubrum* shoot die-back has started in the 50% invasive communities, as its height was decreasing by September 2006. These differences indicate that interspecific competition with *A. platanoides* likely inhibits *A. rubrum* growth at the sapling life-stage. However, the mechanisms for the negative effects that we describe are largely unknown. Some have suggested allelopathy may facilitate the success of *A. platanoides* when competing with natives (Sauer, 1998; Wyckoff & Webb, 1996), but a recent study from the same region as this experimental site indicated allelopathy was unlikely (Rich, 2004).

Also, for *Ulmus americana*, it appears that the presence of *A. platanoides* at the sapling community level will inhibit its growth over time, though these saplings had the highest survival of all species and were likely too young to be affected by Dutch Elm Disease (DED) (Stack *et al.*, 1996). We expect that DED will eventually infect these *U. americana* saplings and change the trajectory of the communities where this tree species is present. While similar growth trends for *Quercus rubra* were not statistically significant, they may still be biologically important.

In addition to competitive effects from invasive saplings, the invasive canopy (*i.e., A. platanoides* canopy) negatively affected native plant growth. In the last sample period, native saplings were 28% shorter beneath the invasive canopy compared to a

native canopy. It appears that the interaction between sapling communities and canopy type may be important for the trajectory of forest structure. Beneath a native canopy, the absence of invasive saplings significantly increased native growth, but the invasive canopy had such a strong negative effect on growth that the presence of invasives in the understory had no impact on native saplings. If this trend holds over time, it seems only an absence of *A. platanoides* in both the understory and canopy will provide optimal native sapling growth. However, in a forest with a native canopy, our study has shown that the absence of invasive saplings will increase the growth of natives, which could enhance the presence of native trees in the future canopy. This information could help guide management decisions regarding invasive removal and augmenting native species growth. Nevertheless, the strong competitive effects of *A. platanoides* at the sapling and canopy levels predict that native saplings will be inhibited by the invasive, either through one or both levels.

The ability of an invasive canopy to suppress native understorey growth has been shown (Martin, 1999; Wyckoff & Webb, 1996) through negative effects of deep shade (Reinhart *et al.*, 2006b), and invaded (Howard *et al.*, 2000), mesic microenvironments (Bertin *et al.*, 2005; Howard *et al.*, 2000). While we found that native plants responded positively to higher light percentages at the sapling level (1.5 m from ground), there was no difference in light beneath the invasive and native canopies. Therefore, it is likely that other variables we did not measure, such as light quantity (photosynthetically active radiation) and quality (Red:Far Red light ratio) (Ammer, 2003; Reinhart *et al.*, 2006b), were important in the negative impact of the invasive canopy.

In a related greenhouse study, *A. rubrum* seedlings had significantly less (32 %) above-ground biomass when grown in soil collected from beneath a mature stand of *A. platanoides* (basal area = 48.5 m^2/ha) than from a mixed native stand (51.4 m^2/ha) (S. Galbraith-Kent, *unpublished data*). Some have suggested that soils already invaded

(Howard *et al.*, 2000) and with a high moisture content (Howard *et al.*, 2000; Reinhart *et al.*, 2006a) may increase invasive growth at the expense of native plants. Though we did not measure soil moisture, we found our native saplings responded positively to thinner leaf litter layers, which may have contributed to a drier microenvironment more favorable to native growth.

Converse to the native species, *A. platanoides* grew similarly in treatments where it comprised two different proportions (25%, 50% of saplings) and beneath both canopy types [*i.e.,* invasive (conspecific) and native]. The capability of *A. platanoides* to inhibit native saplings through both direct competition and overstorey shade effects, while not affecting conspecifics, may contribute to its success in forests. In other studies, soil from different forest types had no effect on *A. platanoides* seedling growth in the greenhouse (S. Galbraith-Kent, *unpublished data*) or in the field (Howard *et al.*, 2000; Reinhart *et al.*, 2006a). It has been shown that when *A. platanoides* is the canopy dominant, soil moisture is increased, which may then promote the understorey success of this invasive species (Reinhart *et al.*, 2006a). In our study, the relative homogeneity (*e.g.,* same land use history, soil type) and proximity of our plots may have contributed to equal *A. platanoides* sapling growth across treatments and canopy type.

In this study, we were solely testing if invasive saplings inhibited the growth of co-occurring native saplings, and if so, at what threshold of invasive proportion does that get expressed. We recognize that the trends we observed of these long-lived species were over just 3 growing seasons and could change over the next several decades. Additionally, asymmetric competition was likely in our study, as the invasive species appeared to have a strong negative effect on the natives, while the natives had little or no negative effect on *A. platanoides*. Nevertheless, the negative effects on native sapling growth by *A. platanoides* (at both the understorey and overstorey canopy levels) cannot be overlooked and should affect future native performance. Even when *A.*

platanoides was present in proportions equal to *A. rubrum* and *U. americana* (*i.e.,* 25% invasive treatment) (Table 1), both native species grew significantly less than when the invasive was not present.

Many studies have investigated the factors that promote invasive success (Aronson *et al.*, 2007; Lundgren *et al.*, 2004), but we wanted to gain insight into what happens when the invasive and native species co-exist in forest understorey communities. Based on our study, we suggest that management of forests with similar proportions of non-reproductive *A. platanoides* saplings could include episodic removals of every 2-3 years. This could give the native saplings opportunities to be released from competition with the invasives and increase in growth. Also, since *A. platanoides* needs several years to mature before reproducing, unlike many herbaceous invasive species (*e.g., Microstegium vimineum, Alliaria petiolata*), annual removal may not be essential. High frequencies of *A. platanoides* removals are not only resource (*i.e.,* labor, funds) intensive, but they may promote the spread of the target invasive species, as well as additional invasives (Webb *et al.*, 2001). While seedlings can be hand-pulled, saplings must be cut, hacked, and have an application of a systemic herbicide (*e.g.,* glyphosate) with follow-up treatments, because cutting alone is often ineffective (Webster *et al.*, 2006). Though our results are based on one invasive tree species, our findings could be applicable to others. We encourage studies that also use an experimental approach to test and quantify competitive effects of invaders on native species.

In conclusion, we have described a study testing interspecific competition between native and invasive saplings in experimental communities within the understorey of an eastern US forest. We found that the presence of *A. platanoides* saplings*,* at proportions both equal to and greater than native trees, will reduce native species growth. Additionally, native plants grew significantly less under an invasive canopy compared to a native canopy, so it appears that optimal native sapling growth

will likely occur only in the absence of *A. platanoides* in both the understory and canopy. However, beneath a native canopy, the absence of invasive saplings did facilitate native growth and this information could help guide management decisions in similar forests. Further research combining field experiments and observational studies testing other community effects and mechanisms, such as mycorrhizal relationships (Stinson *et al.*, 2006) and shade (Reinhart *et al.*, 2006b), would advance our understanding of the interactions between invasive and native species. This knowledge may help make pragmatic and informed improvements in how we should manage for an invader in a specific region.

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Table 1. Experimental design of the planted tree community plots in the understory of a post-agricultural secondary forest in Somerset County, NJ. The number of plants of each species per plot are shown per treatment (0%, 25%, and 50% invasive). The number of plants per plot (n=36) was equal for each of the 15 plots.

Species	Plot Treatment Type (% invasive) [a]		
	0%	25%	50%
Acer platanoides	0	9	18
A. rubrum	12	9	6
Quercus rubra	12	9	6
Ulmus americana	12	9	6
Total number of plants / plot	36	36	36

[a] Dimensions of each plot were 4m x 4m; n=5 plots per treatment.

Table 2. Statistical results from the Repeated Measures MANOVA (multivariate analysis of variance) evaluating the effects of Time, Treatment, Species, Canopy dominant species, and those interactions, on mean native plant height and volume in tree sapling communities. The dependent variables for each MANOVA were the mean values for each of the four sampling periods (2004, 2005, June 2006, September 2006).

Effect	Mean native tree sapling height (cm)			
	Pillai	*df*	F	*P*
Time	0.6084	3, 343	177.77	**< 0.0001**
Canopy dominant [b, c, d]	-	1, 345	21.81	**< 0.0001**
Species [b, e]	-	2, 345	130.73	**< 0.0001**
Treatment [b, f]	-	2, 345	4.02	**0.0188**
Canopy dominant * Species [b]	-	2, 345	1.18	0.3098
Canopy dominant * Treatment [b]	-	2, 345	8.30	**0.0003**
Species * Treatment [b]	-	4, 345	0.37	0.8275
Canopy dominant * Species * Treatment [b]	-	4, 345	1.70	0.1495
Time * Canopy dominant	0.1750	3, 343	24.25	**< 0.0001**
Time * Species	0.1095	6, 688	6.64	**< 0.0001**
Time * Treatment	0.0956	6, 688	5.75	**< 0.0001**
Time * Canopy dominant * Species	0.0127	6, 688	0.74	0.6214
Time * Canopy dominant * Treatment	0.0256	6, 688	1.49	0.1795
Time * Species * Treatment	0.0307	12, 1035	0.89	0.5536
Time * Species * Treatment * Canopy dominant	0.0307	12, 1035	0.89	0.5545

Effect	Mean native tree sapling volume (cm^3) [a]			
	Pillai	*df*	F	*P*
Time	0.8033	3, 343	466.81	**< 0.0001**
Canopy dominant [b, c, d]	-	1, 345	18.77	**< 0.0001**
Species [b, e]	-	2, 345	66.63	**< 0.0001**
Treatment [b, f]	-	2, 345	3.44	**0.0332**
Canopy dominant * Species [b]	-	2, 345	1.36	0.2590
Canopy dominant * Treatment [b]	-	2, 345	5.50	**0.0045**
Species * Treatment [b]	-	4, 345	0.45	0.7757
Canopy dominant * Species * Treatment [b]	-	4, 345	0.89	0.4702
Time * Canopy dominant	0.1437	3, 343	24.25	**< 0.0001**
Time * Species	0.3736	6, 688	26.34	**< 0.0001**
Time * Treatment	0.0794	6, 688	4.74	**< 0.0001**
Time * Canopy dominant * Species	0.0083	6, 688	0.48	0.8251
Time * Canopy dominant * Treatment	0.0294	6, 688	1.71	0.1160
Time * Species * Treatment	0.0182	12, 1035	0.53	0.8993
Time * Species * Treatment * Canopy dominant	0.0283	12, 1035	0.82	0.6275

[a] Since we did not destructively sample the saplings for biomass, we calculated volume as an approximation by using the geometric formula for a right circular cone (plant volume = 1/3*pi*h*r1*r2). This shape is similar to the plant shapes for each species.

[b] Between-subjects effects do not receive a Pillai value.

[c] Canopy dominant and its interactions were treated as random effects. The other three main effects (Time, Species, Treatment) were fixed factors.

[d] Canopy dominant (n=2) = invasive or native canopy

[e] Native species (n=3) = *Acer rubrum, Quercus rubra, Ulmus americana*

[f] Plot treatment (n=3) = 0%, 25%, and 50% invasive communities

Mean values signficant at the *P* < 0.05 level are shown in bold face; 'Pillai' is Pillai's statistic for MANOVA.

n = 363 total native tree saplings

Table 3. Statistical results from the Least Squares Means tests evaluating differences of native plant height and volume per treatment type. The dependent variables for each test were the mean values for each of the three treatments (0%, 25%, and 50% invasive). Mean values are shown (1 SE).

	Tree sapling community plot treatment (% invasive)		
Sampling period	0% (n=5 plots)	25% (n=5 plots)	50% (n=5 plots)
Mean native tree height (cm)			
2004 September	69.4 (1.81) [a]	68.0 (2.10) [a]	67.7 (2.46) [a]
2005 September	91.2 (2.59) [a]	83.4 (2.71) [a,b]	81.2 (2.83) [b]
2006 June	112.9 (3.39) [a]	97.5 (3.51) [b]	91.6 (3.25) [b]
2006 September	119.7 (3.84) [a]	101.1 (3.84) [b]	92.9 (3.25) [b]
Mean native tree volume (cm^3)			
2004 September	32,997 (1,933) [a]	29,982 (2,072) [a]	32,800 (3,517) [a]
2005 September	99,952 (6,553) [a]	75,118 (5,846) [b]	81,075 (6,908) [a,b]
2006 June	228,754 (16,393) [a]	162,835 (18,259) [b]	156,170 (15,546) [b]
2006 September	275,741 (23,959) [a]	177,197 (20,359) [b]	166,343 (20,856) [b]

Since we did not destructively sample the saplings for biomass, we calculated volume as an approximation
  by using the formula for a right circular cone [plant volume (cm^3) = 1/3*pi*h*r1*r2], which is similar to the plant
  shapes for each species.
Means per row with the same letter are not significantly different at the $P < 0.05$ level
Native tree species: *Acer rubrum, Quercus rubra, Ulmus americana*
n = 363 total native tree saplings

Table 4. Linear regression analyses evaluating the ability of each plot variable to significantly predict the response variable. The response (dependent) variable was the mean native sapling height per plot in September 2006 and was $\log_{10}$ - transformed to increase normality. Predictor variables were either $\log_{10}$ or arc-sine transformed.

Plot predictor variable	R^2	relationship to mean height	equation best predicting $\log_{10}$ mean plant height	P
Microstegium vimineum cover [a]	0.0608	+	-0.3523 + 1.197(arc-sine Micro cover)	**< 0.0001**
total plant species richness in plot [a]	0.0415	-	2.191 - 0.3167($\log_{10}$ plant richness)	**< 0.0001**
% light	0.0947	+	1.629 + 0.3514(arc-sine light)	**< 0.0001**
Leaf litter depth (December 2006)	0.1152	-	2.6366 - 0.8973($\log_{10}$ leaf litter depth)	**< 0.0001**
NSS volume (cm^3) [b]	0.0311	-	2.5683 - 0.0843($\log_{10}$ NSS volume)	**0.001**
NSS distance (cm) [b]	0.0715	-	2.2211 - 0.1689($\log_{10}$ NSS distance)	**0.005**
NTS distance (cm) [c]	0.0135	-	2.0892 - 0.0924($\log_{10}$ NTS distance)	**0.03**
NTS dbh (in) [c]	0.0991	+	1.7627 + 0.1143($\log_{10}$ NTS dbh)	**< 0.0001**
pH	0.0001		2.0477 - 0.0754($\log_{10}$ pH)	0.88
Phosphorus	0.0101		1.9076 + 0.0588($\log_{10}$ Phosphorus)	0.06
Iron	0.0327	+	0.4546 + 0.6614($\log_{10}$ Iron)	**0.0005**
Organic matter %	0.0002		1.9842 + 0.0174(arc-sine Organic matter)	0.79
Nitrate	0.0239	+	1.9527 + 0.0385($\log_{10}$ Nitrate)	**0.003**
Ammonium	0.0320	+	1.9114 + 0.0619($\log_{10}$ Ammonium)	**0.001**

[a] prior to planting of plots
[b] NSS = nearest shrub species
[c] NTS = nearest tree species
Native sapling species = *Acer rubrum, Quercus rubra, Ulmus americana*
% light = 100 - % canopy cover

Fig. 1

(a)

Acer platanoides
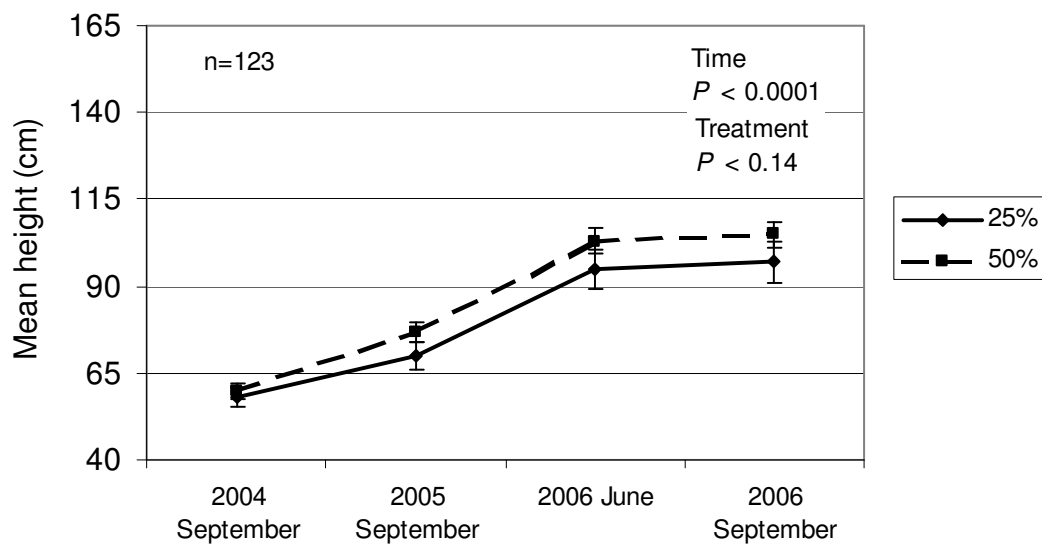
(b)

Acer rubrum

(c)
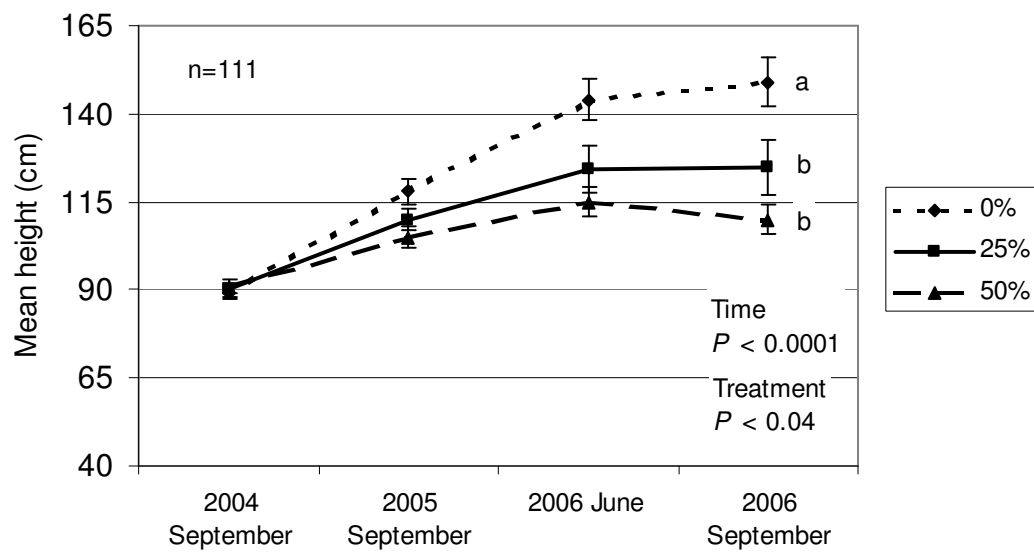
Quercus rubra
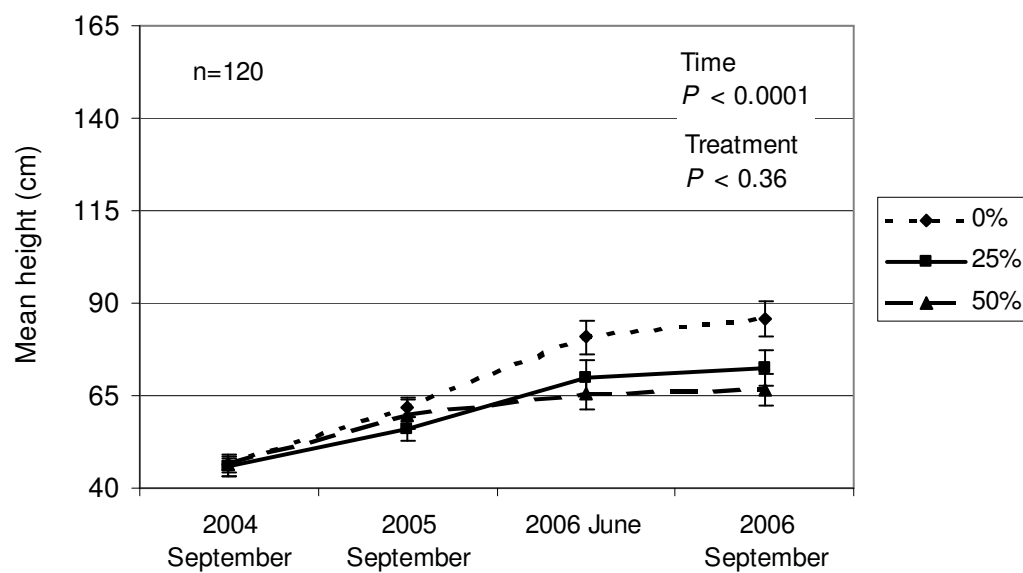
(d)
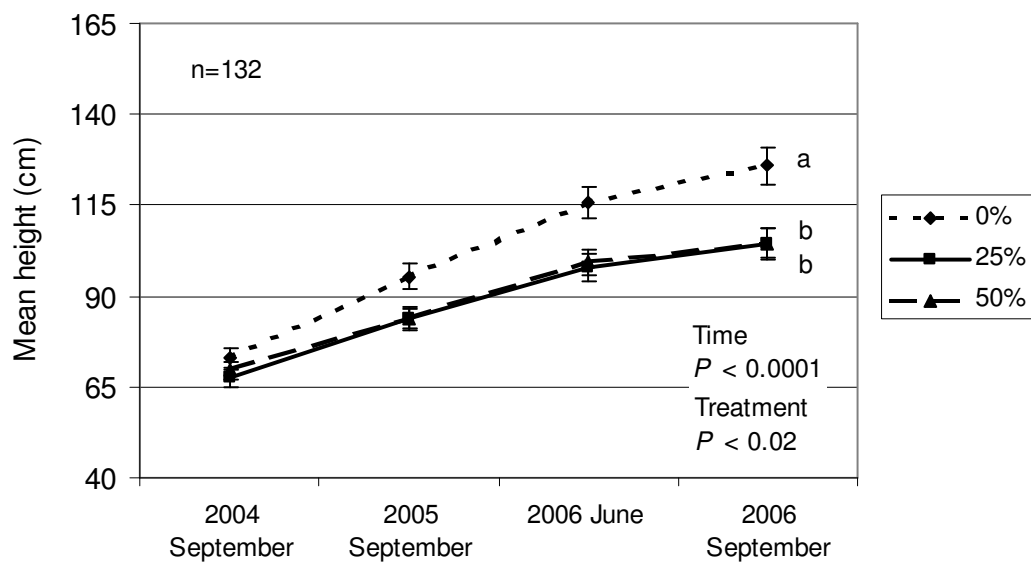
Ulmus americana

Figure 1. Statistical analyses evaluating the effect of Time and Treatment on mean species heights [(a) *Acer platanoides*, (b) *A. rubrum*, (c) *Quercus rubra*, (d) *Ulmus americana*] using a Repeated Measures MANOVA (Pillai's Trace test). The dependent variables were the mean heights for each of the sampling years. Treatments are 0%, 25%, and 50% invasive species (*i.e., A. platanoides*) abundance per plot (see Table 1 for planting design). Between-treatment comparisons that are significantly different are shown with different letters, as identified through the Least Squares Means tests (Tukey option). Mean values $\pm$ 1 SE and sample number are shown per species.

Fig. 2
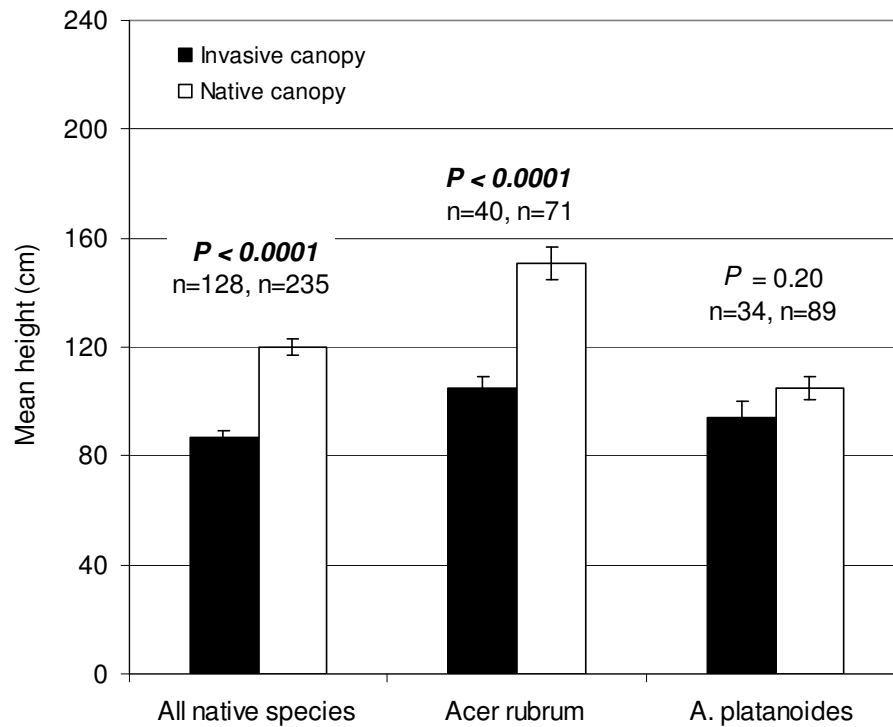
Figure 2. Analyses of variance evaluating the effect of the existing Canopy dominant species (invasive or native) on mean sapling height (in 2006 September) for all native species (*i.e., Acer rubrum, Quercus rubra, Ulmus americana*) and both *Acer* species. Saplings beneath an invasive canopy (*i.e., Acer platanoides*) are represented in black bars, while the white bars show saplings with a native species as the canopy dominant [including *A. rubrum, Fraxinus americana, Quercus alba, Q. palustris,* and *Pseudotsuga menziesii* (horticultural artifact on forest edge)]. Mean values $\pm$ 1 SE, level of significance, and the number of saplings per analysis are given.

Fig. 3

(a)

(b)

Figure 3. Statistical analyses evaluating the effect of sapling community Treatment (invasive or native community), within each of the two Canopy dominant types (invasive or native canopy), on (a) mean relative change in height and (b) mean sapling height (in 2006 September). Communities that contain only native saplings (0% invasive) are shown as light bars, while communities with invasive saplings (25% and 50% invasive) are represented as dark bars (see Table 1 for community planting design). The invasive canopy dominant species was *Acer platanoides,* while several native species were canopy dominants, depending on the plot [including *A. rubrum, Fraxinus americana, Quercus alba, Q. palustris,* and *Pseudotsuga menziesii* (horticultural artifact on forest edge)]. Mean values $\pm$ 1 SE, level of significance, and the number of saplings per analysis are given.

Fig 4.

(a)

(b)

Figure 4. Statistical analyses evaluating the effect of sapling community type (invasive or native community), within each of the two Canopy dominant types (invasive or native canopy), on (a) mean relative change in *A. platanoides* height and (b) mean *Acer platanoides* sapling height (in 2006 September). Communities with *A. platanoides* comprising 25% of the saplings are shown as dashed horizontal bars, while communities with 50% of the saplings being *A. platanoides* are represented with vertical striped bars (see Table 1 for community planting design). The invasive canopy dominant species was *Acer platanoides,* while several native species were canopy dominants, depending on the plot [including *A. rubrum, Fraxinus americana, Quercus alba, Q. palustris,* and *Pseudotsuga menziesii* (horticultural artifact on forest edge)]. Mean values $\pm$ 1 SE, level of significance, and the number of saplings per analysis are given.

CHAPTER 2

Interactions between the invasive *Acer platanoides* (Norway maple) and native *A. rubrum* (red maple): effects of interspecific competition and soil type on seedling growth

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ABSTRACT

Invasive species continue to alter the plant communities of the eastern United States. To better understand the mechanisms and characteristics associated with invasive success, it is helpful to study competition between congeneric species. In a greenhouse study, we investigated (1) the effect of forest soil type (*i.e.,* collected beneath an invasive and native stand) on seedling growth of the invasive *Acer platanoides* (Norway maple) and native *A. rubrum* (red maple), and the (2) effects of full and partial interspecific competition on species growth.   We hypothesized that *A. rubrum* would grow better in the native soil and with conspecific seedlings, but that A. platanoides would perform better in the invasive soil. We found *A. rubrum* seedling growth was negatively affected by soil from the invaded stand, as it had lower above-ground (32%) and below-ground (26%) biomass, and number of leaves (20%) than in the native soil. We found the root:shoot resource allocations of *A. platanoides* depended on soil type, as it had 14% greater root:shoot mass allocation in the native soil, which may indicate a mechanism based on optimal resource partitioning contributing to its ecological success. With a large ecological amplitude, *A. rubrum* may be a useful species for ecological restoration where *A. platanoides* has been present. However, the impacts of *A. platanoides* on soil functioning and plant interactions must be addressed before protocols for reintroducing native tree species can be refined.

KEYWORDS

Acer platanoides, Acer rubrum, growth allocation, interspecific competition, invasive species, soil effects

INTRODUCTION

The impact of biological invasions has been discussed for several decades (Elton, 1958; Vitousek *et al.*, 1996) with the effects on wholesale natural resources, native biodiversity, and ecological functioning of primary concern (Mack *et al.*, 2000). Many studies have used various measures to compare how native and invasive non-native plants perform when they occur together (Daehler, 2003), but the mechanisms of how most non-native plants invade, establish, and become successful components of ecosystems are still not well understood (Levine *et al.*, 2003).

It is often assumed that many species are invasive due to greater growth rates (Sanford *et al.*, 2003; Webster *et al.*, 2005), competitive abilities (Gorchov & Trisel, 2003; Hager, 2004), escape of natural predators (Cappuccino & Carpenter, 2005; Reinhart & Callaway, 2006), and increased resource or disturbance levels (Daehler, 2003). Adding additional complexity, some invasions may result from a discrete event in time (*e.g.,* increased propagule pressure) (Lockwood *et al.*, 2005), while others may be due to characteristics of a specific location or the invasive species itself (Blackburn & Duncan, 2001; Lockwood *et al.*, 2005).

The modification of soil functioning by invasive species has been documented for several plants including *Berberis thunbergii* DC. (Ehrenfeld, 2003; Ehrenfeld *et al.*, 2001), *Myrica faya* (Ait.) Wilbur (Vitousek *et al.*, 1987), *Alliaria petiolata* [Bieb] Cavara & Grande (Stinson *et al.*, 2006), *Centaurea* spp. (Bais *et al.*, 2003; Callaway & Aschehoug,

2000) and others (Reinhart & Callaway, 2006). Litter from invasive plants can alter soil

properties by increasing pH (Ehrenfeld *et al.*, 2001; Kourtev *et al.*, 1998), nitrification

rates (Ehrenfeld *et al.*, 2001; Vitousek *et al.*, 1987), decreasing litter depth and organic

soil matter (Kourtev *et al.*, 1998), changing the soil microbial communities (Kourtev *et al.*,

2003; Reinhart & Callaway, 2006), and raising the local decomposition rate (Ashton *et

al.*, 2005; Ehrenfeld, 2003).

   Acer platanoides (Linn.) is a European invasive species that was intentionally

introduced in North America in 1756 (Nowak & Rowntree, 1990), and has continued to

spread in eastern (Martin, 1999; Webb *et al.*, 2000), midwestern (Wangen *et al.*, 2006),

and western (Reinhart *et al.*, 2005) North American forests. As was the case then, it is

still used as an ornamental street tree for its deep shade, tolerance to disturbed soils,

and aesthetics (Meiners, 2005; Webb *et al.*, 2001), though its use by the nursery trade

seems to be declining (S. Galbraith-Kent, personal observation).

   The high recruitment and persistence of *A. platanoides* in open and closed

forests is typically much greater than native species, which causes concern for the

structure of future forests (Martin, 1999; Sanford *et al.*, 2003; Wyckoff & Webb, 1996).

Microenvironments beneath canopies of *A. platanoides* have been shown to limit native

seedling proliferation, as the invasive adults facilitate conspecific seedling growth and

reproduction (Martin, 1999; Reinhart *et al.*, 2006a; Wyckoff & Webb, 1996), by increased

shade (Reinhart *et al.*, 2006b), soil moisture (Reinhart *et al.*, 2006a), efficient use of

resources (Kloeppel & Abrams, 1995), and possible allelopathic effects on other species

(Sauer, 1998), though that mechanism was not experimentally supported (Rich, 2004).

   Most studies observing the dynamics of *A. platanoides* with another species have

done so using the native *Acer saccharum* (Marsh.), which is another shade-tolerant,

late-successional tree (Martin, 1999; Meiners, 2005; Webb *et al.*, 2001). *A. saccharum*

seedlings and saplings are typically out-competed by its congener (Martin, 1999) and

have greater growth beneath an overstory lacking the invasive (Webb *et al.*, 2001). Another native maple, *Acer rubrum* (Linn.), is the most abundant and widespread tree species in eastern North America (Harlow *et al.*, 1996). *A. rubrum* can persist on a wide range of soil types and elevation, is found in diverse sites from dry ridges to swamps (Walters & Yawney, 1990), and has continued to increase in importance in eastern forests (Abrams, 1998; Dodge, 1997; Galbraith & Martin, 2005). With the proliferation of *A. platanoides* across varied forest types, we suggest that *A. rubrum* may be a good study species and candidate when considering realistic restoration goals in eastern forests containing *A. platanoides*.

In this greenhouse study, we evaluated the interaction of *A. platanoides* and *A. rubrum* seedlings by testing the effects of (1) soil type and (2) location (above-ground, below-ground, both) and type (intraspecific, interspecific) of competition on seedling growth. Based on studies that have shown invasives change soil functioning (Ehrenfeld, 2003; Ehrenfeld *et al.*, 2001), we hypothesized that *A. rubrum* would grow better in non-invaded forest soil, while *A. platanoides* would have greater growth in invaded forest soil.

There have been relatively few experiments that have used woody species to test the effects of above- and below-ground competition and resource partitioning, as most have used grass (Cahill, 2003) and leguminous species (Aerts *et al.*, 1991; Gersani *et al.*, 2001; Murphy & Dudley, 2007). Our study tested the ability of *A. rubrum* to directly compete with *A. platanoides*, as measured by growth performance. Based on other studies of facilitation (Reinhart *et al.*, 2006a; Wyckoff & Webb, 1996) and species ecology (Meiners, 2005), we hypothesized that *A. platanoides* would have greater overall growth than *A. rubrum* and that both species would grow best with a conspecific seedling when competing simultaneously above- and below-ground.

METHODS

This greenhouse study compared the growth of *Acer platanoides* and *A. rubrum* seedlings in planted pots with soil collected from two different forest stands (native and invasive canopies) and in six different competition treatments.

Collection site

We used field soil and *Acer platanoides* seedlings collected from a post-agricultural secondary forest in the Piedmont of central New Jersey (Somerset County, NJ). This forest is located on the property of Duke Farms (1093 ha total) (N 40˚33.8′ W 74˚25.4′) where soils are deep (<200 cm to fragipan) and loamy. The primary soil type is Dunellen sandy loam (3 to 8% slopes), with secondary soils of Lamington silt and Penn silt loam (0 to 2%, 2 to 6% slopes, respectively) (Natural Resources Conservation Service 2007). The first stand (0.36 ha = 3600 m^2) had an overstory canopy (stems > 2.5 cm dbh) primarily dominated by native trees, which aligned with historical descriptions of mixed oak forests in the area (Braun, 1950; Collins & Anderson, 1994; Monk, 1961): *Quercus alba* L. (relative IV=19.2%), *A. rubrum* (relative IV=16.9%), and *Q. palustris* Muenchh. (relative IV=14.5%) (S. Galbraith-Kent, *unpublished data*). Although *A. platanoides* was present in the canopy, its relative importance (11%) was low compared to native species. The understory was primarily composed of defined patches of the invasive grass, *Microstegium vimineum* Trin. Camus and the shrub, *Berberis thunbergii* DC. The second stand (0.04 ha = 400 m^2) was located 150 m from the first stand and its canopy was dominated by *A. platanoides* (relative importance = 74%) (S. Galbraith-Kent, *unpublished data*). In the understory, this stand was densely composed of *A. platanoides* seedlings and sparse patches of *M. vimineum* on the edges. We will refer to these areas by their dominant canopy types as the "native" and "invasive" stands, respectively.

Plant material

A. *platanoides* seedlings of similar size were collected from the invasive stand on July 5 (2006). We used *A. rubrum* seedlings that were collected as seeds from naturally occurring populations within the region and grown in a native plant greenhouse, since there were few *A. rubrum* seedlings in the forest. All seedlings had germinated during 2004 and were approximately two years of age. Roots of neither species were sterilized, as we wanted to minimize seedling mortality. However, to enhance the efficacy of the soil treatment, the pre-existing soil on all roots was removed as much as possible (without disturbing root integrity) before seedlings were used in the experiment.

Soil collection

On July 3 (2006), field soil was collected (0-10 cm depth) from three randomly selected areas in the invasive stand (0.04 ha = 400 m^2), and three points in the native stand (0.36 ha = 3600 m^2). In the native stand, soil was collected beneath a native tree, at least 8 m from the nearest *B. thunbergii* shrub, and in an patch where *M. vimineum* was absent, to minimize possible confounding factors, as both invasive species can alter soil chemistry and function (Ehrenfeld *et al.*, 2001; Kourtev *et al.*, 2003; Kourtev *et al.*, 1999).

Design of experiment

We used a 2 x 6 factorial design with two Soil types and six Competition treatments as the main factors (Fig. 1). There were a total of 120 pots (240 seedlings = 120 *A. platanoides*, 120 *A. rubrum*), with 60 pots per soil type (invasive, native) equally distributed among the competition treatments. There was zero seedling mortality across all treatments and replicates, which helped maintain a balanced design the duration of the experiment. To test the effects of direct competition on growth between both *Acer*

species, we used six plant pot treatments: Intraspecific Full competition (*Acer platanoides* only), Intraspecific Full competition (*A. rubrum* only), Interspecific Full competition (both *Acer* species), Interspecific Above competition, Interspecific Below competition, and Interspecific None (Table 1) (Fig. 1). All pots had the same volume (3635 cm^3) and two seedlings to maintain equal density.

Competition treatment. For Interspecific pot treatments with partial or absent competition (*i.e.,* Above, Below, None), barriers were used to establish the specific condition (Table 1) (Fig. 1). A barrier bisected an individual plant pot and was constructed from pieces of blue opaque commercial plastic tarp attached to the inside walls and bottom of the pot with standard commercial duct tape and, for the above-ground barriers, wooden dowels (3mm diameter). The dimensions of root (16.5cm wide x 17cm tall), shoot (16.5cm x 70cm), and combined (16.5cm x 90cm) barriers were cut to fit the 1-gallon individual plant pots (16.5cm diameter and 17cm tall) and at a maximal height that allowed only the intended competition interaction (*e.g.,* shoot barriers that prevented above-ground competition, but allowed root competition) between the seedlings. For each pot, the barrier treatment was constructed and installed first, and then two seedlings were added along with one of two soil treatments described below.

Soil treatment. Field soil was mixed to a 1:1:1 ratio with sterile, commercial silica play sand and sterile potting soil; these two mixtures were used to fill individual pots. Using equal parts of the two sterile substrates is common in greenhouse experiments. All tools used to combine soils were sterilized with a bleach solution between treatments.

Data collection

This experiment was initiated on July 6 (2006), when all pots were randomly placed in the greenhouse. All pots were kept in the greenhouses and received equal amounts of water (watered 3-4 times weekly), so that the soil remained moist. We

rotated pots bi-weekly to minimize any confounding effects of bench placement and neighbor shading on growth. All seedlings were measured for height at weeks 2, 8, and 14, while leaf number was recorded at week 14. The experiment was completed after 14 weeks (during the week of October 16) and all parts per plant were harvested into groups of leaves and stems (above-ground biomass) and roots (below-ground biomass). All harvested material was dried for approximately 48 hours at 70°C until a constant weight. The five growth variables analyzed per plant were: (1) final above-ground biomass; (2) final root biomass; (3) final leaf number; (4) root:shoot mass ratio (root mass/shoot mass); and (5) relative height growth rate [RGR = $(\log_{10}$ (final height / initial height)) / T] for height was calculated using T = 98 days, the length of the experiment (Beckage & Clark, 2003; George & Bazzaz, 1999).

Soil characteristics

We collected soil (0-10 cm depth) from the two forest stands on December 7 (2006), to test for differing characteristics between the stands. Our methodology was analogous to the soil collection done in July, described above. Our samples were analyzed for chemical and textural characteristics by the Rutgers Soil Testing Laboratory (Middlesex County, New Jersey).

Statistical analyses

Soil characteristics were tested for differences between the two forest collection stands (*i.e.,* invasive, native) using analysis of variance (ANOVA), with stand as a fixed factor. Levene's test for homogeneity of variances was used and transformations ($\log_{10}$ and arc-sine) were calculated, but the data remained heterogeneous. However, we were confident to use these tests, as the *F*-statistic has been shown to be robust to departures from normality and variance homogeneity (Underwood, 1997).

The effects of seedling Species (*A. platanoides* and *A. rubrum*) and Soil type on the five growth variables were tested using a multivariate analysis of variance (MANOVA) with fixed factors (Species and Soil) (PROC GLM, General Linear Model, Pillai's Trace tests). While Wilks lambda is the most commonly used test-statistic in MANOVA, we used Pillai's Trace, which is more forgiving to violations of normality (Gotelli & Ellison, 2004). An ANOVA was used to analyze dependent variables once a significant effect was identified with the MANOVA. Even though assumptions for normality and variance homogeneity were not met after log_{10} - transformations, the *F*-statistic is robust, particularly in experiments with large samples (n > 5) that are balanced (Underwood, 1997).

We did similar analyses testing the effects of Competition type on species growth, but based on reviewer comments, the tests were done in two different groups. Because the three treatments with partial or absent competition (*i.e.,* Interspecific Above, Interspecific Below, Interspecific None), had barriers reducing available pot volume to both plants, these treatments were analyzed separately from the full competition treatments.

All mean and standard error values in tables and figures are original (non-transformed) units. Instead of reporting relative growth rate means, we report means as percentage height increases to increase the clarity of species trends. All analyses were done with SAS version 9.1 for Windows (SAS Institute, Cary, NC, USA).

RESULTS

The invasive forest stand dominated by *A. platanoides* had a smaller percentage of organic matter and sand in the soil, as were several of the other soil micronutrients we measured, except for a significantly greater amount of phosphorus (Table 2).

From the overall MANOVA, we found highly significant effects of Species (Pillai = 0.72, $F_{5, 216}$ = 111, $P < 0.0001$), Soil type (Pillai = 0.16, $F_{5, 216}$ = 8.04, $P < 0.0001$), and the Species * Soil type interaction (Pillai = 0.09, $F_{5, 216}$ = 3.99, $P = 0.0018$), on the five growth variables: above-ground biomass, root biomass, leaf number, root:shoot mass ratio, and relative height growth rate (RGR). Additionally, we compared *Acer platanoides* and *A. rubrum* across all treatments and found the species to significantly differ for all measured variables, except for the change in height (RGR *A. platanoides* = 0.0024 $\pm$ 0.00012, RGR *A. rubrum* = 0.0026 $\pm$ 0.00018) (Table 3). The *A. rubrum* seedlings had an above-ground biomass more than three times greater than that of *A. platanoides*, twice the root biomass, and more than four times the number of leaves ($P < 0.0001$ per variable). *A. platanoides* seedlings had the lower values for four of the five variables, but a mean root:shoot mass ratio that was 52% greater than its native congener (Table 3). Although we chose seedlings of relatively equal sizes in the beginning of the experiment, the starting height of *A. rubrum* (11.3 $\pm$ 0.2 cm) was greater than *A. platanoides* (10.4 $\pm$ 0.2 cm) ($F_{1, 238}$ = 7.6, $P = 0.006$), which may have given the native maple a slight initial advantage.

Acer rubrum

There was a strong Soil effect on *A. rubrum* seedling biomass, as there was a 46% greater above-ground and 36% greater root biomass in soil from the native stand, when compared to the soil from the invasive stand (Table 4). There was also a lower leaf number in the latter stand, but neither the root:shoot mass ratio nor seedling height change differed based on Soil type.

Competition between *A. platanoides* and *A. rubrum* seedlings was evaluated using two groups of analyses to test hypotheses of (1) greater growth in the Intraspecific Full than the Interspecific Full treatment (Table 5A) and (2) greater Interspecific growth

in the treatment with no competition (Table 5B). For *A. rubrum*, there were overall

differences in growth variables between the two Full competition treatments (Pillai =

0.56, *P* < 0.0001) (Table 5A), but not among the three Interspecific treatments testing

partial or absent competition (Pillai = 0.27, *P* = 0.1186) (Table 5B). *A. rubrum* seedlings

had higher above-ground biomass, root biomass, leaf number, and relative height

growth, when grown in full competition with *A. platanoides* than in full competition with

another *A. rubrum* seedling.

Acer platanoides

      The root:shoot mass ratio for *A. platanoides* was significantly greater in the

native soil, but other variables were unaffected by Soil type (Table 4). There were

overall growth differences between the two Full competition treatments (Pillai = 0.22, *P* =

0.0182) (Table 5A), but unlike *A. rubrum*, this species had higher biomass when

competing with a conspecific seedling. There were no growth differences for *A.

platanoides* between treatments with partial or absent competition (Pillai = 0.26, *P* =

0.1375) (Table 5B).

DISCUSSION

      We found that native *Acer rubrum* seedlings grown in invaded soil had

significantly less growth, while invasive *A. platanoides* seedlings increased root

allocation in the native soil. The effects of invasive soil on the native *Acer* echo some of

the current concerns associated with soil alteration by invasive species. The two

species differed in their growth responses between the two full competition treatments

(*i.e.,* Interspecific, Intraspecific), which were likely due to initial seedling heights and high

light availability in the greenhouse. We decided not to use shade cloths, in an effort to

increase seedling survivorship, but this abundance of light likely gave *A. rubrum* a competitive advantage from the beginning.

A. rubrum had greater overall above-ground biomass, root biomass, and number of leaves than *A. platanoides*. These patterns were not expected, since several comparison studies of *A. platanoides* and native *A. saccharum* have found the invasive to have greater growth rates (Kloeppel & Abrams, 1995), understory densities (Martin, 1999; Webb & Kaunzinger, 1993), higher survival in open and understory environments (Sanford *et al.*, 2003) and greater seed mass and overall seedling size (Meiners, 2005). Meiners (2005) used seeds to test species characteristics and found that *A. platanoides* seedlings grew larger than *A. saccharum* because of its greater seed size, as the relative growth rates were similar. He found *A. platanoides* seedlings to be nearly twice the size of the native *Acer*, which was opposite of the trend we found with *A. rubrum*. If we had used seeds, seedlings with the same initial sizes, or a shading regime more similar to forest conditions within the greenhouse, we may have seen the more common and expected differences between the invasive and native *Acer* species, as the rate of seedling height change was the same for *A. platanoides* and *A. rubrum* for the duration of the experiment.

One of our most striking findings was the effect of Soil type on *A. rubrum*. The number of leaves, above-ground biomass, and root biomass of *A. rubrum* seedlings was significantly less when grown in soil from an invasive stand compared to a native stand. Similar patterns have been shown by several field studies in eastern (Martin, 1999; Wyckoff & Webb, 1996) and western forests (Reinhart *et al.*, 2006a; Reinhart *et al.*, 2006b), where native seedling growth and survival is reduced in soil beneath *A. platanoides* canopies.

The response of *A. rubrum* seedlings to invaded soil is similar to studies of known allelopathic species (Bais *et al.*, 2003; Orr *et al.*, 2005), but we did not directly

test for the presence of allelopathic chemicals. Allelopathy (Sauer, 1998; Wyckoff & Webb, 1996) has been suggested as a mechanism for decreased native growth in soils dominated by *A. platanoides* canopies. However, while antifungal chemicals have been identified in its leaves (Dix, 1974), a field and greenhouse study in the same region found that if *A. platanoides* does have allelopathic properties, they are minimal at best (Rich, 2004).

Our *A. rubrum* results possibly indicate growth inhibition or negative plant-soil community feedback in invaded soil (Stinson *et al.*, 2006), positive plant-soil community feedback (Ehrenfeld *et al.*, 2005; Reinhart & Callaway, 2006) within the native soil, or a combination of both. The native stand contained patches of two understory invasives (*M. vimineum and B. thunbergii*) that were absent in the invasive stand and these two species may have also contributed to the Soil effects. But, with greater *A. rubrum* growth observed in soil from the native stand, these understory invasives appear to have had minimal negative impact in this study.

We found two differences in soil chemistry between the stands, which were increased phosphorus and lower organic matter in the invasive stand. The lower *A. rubrum* growth in the invasive stand may have been a response to the greater amount of phosphorus present. Plant uptake of this nutrient is usually through arbuscular mychorrizal fungi (AMF) (Bever *et al.*, 2001) and while altering AMF communities is a mechanism for another invasive species (Stinson *et al.*, 2006), our study did not test for AMF presence. We did find a lower organic matter content in the invasive stand, which is consistent with another study from the same region (Kourtev *et al.*, 1998). Though Ashton et al. (2005) found that *A. platanoides* and *A. rubrum* had similar decomposition rates, *A. platanoides* returned nitrogen to the soil faster than its native congener. This is a positive-feedback mechanism that has increased the success of other invasive species (Ehrenfeld *et al.*, 2001; Vitousek *et al.*, 1987), as growth of native seedlings is reduced.

The decomposition of litter from *A. platanoides* trees in the invasive stand may be an explanatory mechanism for the observed lower growth of *A. rubrum* in this soil. Invasive plants have been shown to change soil microbial communities in as little as three months (Kourtev *et al.*, 2003) in addition to several soil properties, such as pH, % organic matter, and nitrification rates (Ehrenfeld, 2003; Kourtev *et al.*, 1998). Some of the largest *A. platanoides* trees in this invasive stand are at least 50 years old (S. Galbraith-Kent, *unpublished data*), which may be enough time for this invasive species to alter soil functioning and affect seedling growth.

While *A. rubrum* growth was greatly impacted by Soil type, the growth of *A. platanoides* was relatively similar in both soils. In another greenhouse study (Reinhart *et al.*, 2006a), *A. platanoides* seedlings were also unaffected by soil from differing forests. While seedling facilitation under conspecific canopies has been shown for this species in the field (Wyckoff & Webb, 1996) through positive influences of deep shade (Reinhart *et al.*, 2006b), high soil moisture (Reinhart *et al.*, 2006a), and disturbed (Howard *et al.*, 2000), mesic microenvironments (Bertin *et al.*, 2005), we did not find increased *A. platanoides* seedling growth in soil collected beneath a Norway canopy. That said, we feel pattern of invasion and facilitation of *A. platanoides* in the field is due to characteristics stated above and other, landscape and possibly site-specific, issues not addressed in our greenhouse design.

An interesting distinction between the two species was that *A. platanoides* had a greater root:shoot mass ratio in the Mixed native soil, while *A. rubrum* showed no difference between soil types. Optimal resource partitioning (Chapin, 1980) may explain this *A. platanoides* response if soil nutrients and biotic associations that facilitate *A. platanoides* root growth were present in the Norway maple soil, but were absent in the native soil (*e.g.,* lower phosphorus), *A. platanoides* may be responding with greater root biomass due to the soil deficiencies. However, resources may not account for this

difference, as a greater root:shoot mass ratio is often observed for relatively small plants (Cahill, 2003), such as the seedlings we used.

In the competition experiment, we found no growth differences for either *Acer* species among the three treatments with partial (*i.e.,* Above, Below) or absent (*i.e.,* None) competition. The pots of these treatments contained at least one barrier and this may have contributed to increased plant stress (Schenk, 2006), as plants are often able to detect barriers before contacting them, resulting in self-imposed decreased root growth (Falik *et al.*, 2005). Thus, this limited our ability to understand effects of partitioned competition between *A. platanoides* and *A. rubrum* in this study.

However, we did see significant differences between the two full competition (Intraspecific and Interspecific) treatments for both of the *Acer* species. We originally assumed that seedlings would grow better in full competition with conspecifics, rather than seedlings of the other species. Instead, *A. rubrum* seedlings performed significantly greater in the full competition treatment with *A. platanoides*. Niche partitioning could be a possible reason for this result, as *A. platanoides* may utilize different resources than *A. rubrum*. The asymmetric competition between these two species could be due to *A. rubrum* seedlings having a larger initial size at the beginning of the experiment. This may have given the native an advantage over the invasive throughout the experiment, as larger plants typically have a greater competitive effect over smaller individuals (Gaudet & Keddy, 1988). If the seedlings of both species had been the same size, or if *A. platanoides* seedlings had been larger than *A. rubrum*, then we would not predict *A. rubrum* to grow better with a heterospecific.

This skewed result illustrates the importance of field studies (as they incorporate a majority of natural processes), the limitations of greenhouse experiments (which possess unrealistically optimal conditions), and the need to properly integrate information from both sources to increase our understanding. Based on our study, we

are certainly not stating that *A. rubrum* will grow better with *A. platanoides* as competitors, but acknowledge how the initial conditions likely affected outcomes of interspecific competition. Field studies of these two species have shown competitive displacement of *A. rubrum* by *A. platanoides* (Fang, 2003), the suppression of *A. rubrum* recruitment in the presence of *A. platanoides* (Fang, 2005), and decreased numbers of another native *Acer* among *A. platanoides* seedlings in a forest understory (Martin, 1999; Webb *et al.*, 2000). We do not dispute the negative impact of *A. platanoides* on *A. rubrum* in the field as shown by these other studies (including Chapter 1), as additional life history interactions affect community dynamics over time.

Successful regeneration and growth of *A. platanoides* seedlings under a conspecific canopy has been shown in various forests (Martin, 1999; Reinhart *et al.*, 2006a; Wyckoff & Webb, 1996). The environmental modification (*e.g.,* soil moisture, shade) and facilitation by *A. platanoides* on larger scales (Reinhart *et al.*, 2006a; Reinhart *et al.*, 2005) are not applicable to our greenhouse study, though it appears we also observed facilitation at the seedling-level, as two *A. platanoides* seedlings grown together had greater biomass values than when a seedling was grown with an *A. rubrum*.

Based on this greenhouse study, we suggest complementary field experiments to test intraspecific and interspecific competition in invasive and native soils. Also, field studies that test the ability of *A. platanoides* to shift resource allocation based on soil type or microenvironment would be helpful, as we try to understand mechanisms contributing to invasive species success.

We have measured indirect and direct interactions between *A. rubrum* and *A. platanoides* in this greenhouse experiment. In full competition, *A. rubrum* seedlings had a positive biomass response to *A. platanoides* as its neighbor, which was likely due to the initial size advantage of *A. rubrum* and high light conditions. For *A. platanoides*, it

appears facilitation occurred at the seedling level, as its biomass was greater with conspecifics. Also, there was a significant shift to greater root:shoot mass ratio for *A. platanoides* in the native soil, which suggests an ability of the invasive to change energy allocation based on available resources; *A. rubrum* did not show this shift. The lower growth of *A. rubrum* in soil from beneath an invasive canopy is a concern and suggests inhibition through many possible mechanisms (*e.g.,* increased litter decomposition and phosphorus). With its large ecological amplitude, *A. rubrum* may be a useful species for ecological restoration where *A. platanoides* has been present, but we need additional understanding of how this invasive species modifies the soil before protocols for reintroducing native tree species can be refined.

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Table 1. Description of the competition treatments used.

Competition type / Treatment	Any pot barrier(s) present? [a]	Pot barrier type	Species present	# plants per pot
Intraspecific				
Full (*Acer platanoides*)	no	--	*Acer platanoides* only	2
Full (*A. rubrum*)	no	--	*A. rubrum* only	2
Interspecific				
Full	no	--	Both species	2
Above	yes	root barrier	Both species	2
Below	yes	shoot barrier	Both species	2
None	yes	root & shoot barriers	Both species	2

[a] All pots were the same dimensions (16.5 cm diameter and 17 cm tall) and volume (3635 cm^3)

Table 2. Statistical analyses evaluating the effect of forest stand on soil characteristics. Means (+ 1 SE) are shown.

| Characteristic | Forest stand | | F [c] | P |
	Native stand [a]	Invasive stand [b]		
Soil chemistry				
pH	4.3 ± 0.3	4.4 ± 0.3	0.08	0.8
P (mg/kg)	16.5 ± 2.4	45.0 ± 9.09	9.19	**0.04**
K (mg/kg)	87.5 ± 25.3	80.5 ± 11.6	0.06	0.8
Mg (mg/kg)	47 ± 7	40.0 ± 11.5	0.27	0.6
Ca (mg/kg)	260 ± 90	234 ± 41	0.07	0.8
Cu (mg/kg)	3.9 ± 0.6	4.1 ± 0.2	0.11	0.8
Mn (mg/kg)	39.6 ± 6.9	33.2 ± 8.6	0.34	0.6
Zn (mg/kg)	4.6 ± 1.1	3.6 ± 0.6	0.66	0.5
B (mg/kg)	1.1 ± 0.2	0.9 ± 0.3	0.85	0.4
Fe (mg/kg)	227 ± 52	192 ± 28	0.34	0.6
NO_3^- (mg/kg)	7.00 ± 1.41	5.00 ± 0.72	1.59	0.3
NH_4^+ (mg/kg)	4.00 ± 0.69	2.00 ± 0.40	6.22	0.07
Organic Matter (%)	7.36 ± 0.93	4.40 ± 0.30	9.06	**0.04**
Organic Carbon (%)	4.27 ± 0.74	2.55 ± 0.41	4.13	0.1
Soil texture				
Sand (%)	41.7 ± 0.3	37.0 ± 0.00	196.0	**0.0002**
Silt (%)	47.6 ± 0.9	50.7 ± 0.33	10.1	**0.03**
Clay (%)	10.7 ± 0.7	12.3 ± 0.33	5.0	0.09

[a] Native stand (most important species): *A. rubrum* (I.V. = 19.2%), *Quercus rubra* (16.9%), and *Q. palustris* (14.5%).

[b] Invasive stand = *A. platanoides* (I.V. = 73.2%)

[c] df = 1, 4 for each comparison

n = 3 samples for each soil variable

Comparisons significant at the *P* < 0.05 level are in boldface type

ANOVA tests used Type III sums of squares from SAS version 9.1 for Windows

Table 3. Statistical results from the ANOVA testing the effect of species on above-ground biomass, root biomass, leaf number, root:shoot mass ratio, and relative height growth. Mean values are shown $\pm$ 1 SE.

Mean growth variable $\pm$ 1 SE	Acer platanoides	Acer rubrum	F [a]	P
Above-ground biomass (g)	0.93 $\pm$ 0.09	4.03 $\pm$ 0.18	345.58	**< 0.0001**
Root biomass (g)	1.19 $\pm$ 0.08	4.22 $\pm$ 0.17	326.26	**< 0.0001**
Leaf Number	6.06 $\pm$ 0.44	27.2 $\pm$ 0.92	369.56	**< 0.0001**
Root:Shoot mass ratio	1.64 $\pm$ 0.07	1.08 $\pm$ 0.02	67.22	**< 0.0001**
Relative height growth (%) [b]	86.85 $\pm$ 6.90	97.13 $\pm$ 8.03	0.45	0.51

[a] df = 1, 238 (for each variable)

[b] Relative height growth rate (RGR) was statistically analyzed as RGR = (($\log_{10}$ (final height / initial height)) / T),

where T = 98 days (days of experiment duration), but percentage values are shown for clarity

[% growth = (((final height - initial height) /initial height)*100)].

mean values significant at the P < 0.05 level are shown in boldface type

Table 4. Statistical results from the ANOVA testing the effect of soil type (invasive or native) on several species measurements (above-ground biomass, root biomass, leaf number, root:shoot mass ratio, and relative height growth). Meanvalues are shown $\pm$ 1 SE.

	Seedling Species			
	Acer platanoides		Acer rubrum	
	Soil type			
Mean growth variable ($\pm$ 1 SE)	Native [a]	Invasive [b]	Native	Invasive
Above-ground biomass (g)	0.95 $\pm$ 0.12	0.92 $\pm$ 0.12	**4.79 $\pm$ 0.25** ***	**3.27 $\pm$ 0.20**
Root biomass (g)	1.23 $\pm$ 0.11	1.15 $\pm$ 0.12	**4.86 $\pm$ 0.25** ***	**3.58 $\pm$ 0.22**
Leaf Number	6.02 $\pm$ 0.62	6.10 $\pm$ 0.63	**30.3 $\pm$ 1.46** *	**24.1 $\pm$ 0.99**
Root:Shoot mass ratio	**1.76 $\pm$ 0.12** *	**1.51 $\pm$ 0.05**	1.05 $\pm$ 0.03	1.10 $\pm$ 0.03
Relative height growth (%) [c]	86.0 $\pm$ 9.54	87.7 $\pm$ 10.2	95.5 $\pm$ 11.3	98.8 $\pm$ 11.5

[a] Native stand (most important species): A. rubrum (I.V. = 19.2%), Quercus rubra (16.9%),

and Q. palustris (14.5%).

[b] Invasive stand = A. platanoides (I.V. = 73.2%)

[c] Relative height growth rate (RGR) was statistically analyzed as RGR = (($\log_{10}$ (final height / initial height)) / T),

where T = 98 days (days of experiment duration), but percentage values are shown for clarity

[% growth = (((final height - initial height) /initial height)*100)].

* intraspecific comparisons significant at the P < 0.05 level

*** intraspecific comparisons significant at the P < 0.0001 level

Table 5. Statistical results from MANOVA and ANOVA evaluating the effect of competition on growth variables of two seedling species, *Acer platanoides* (Norway maple) and *A. rubrum* (red maple). Two groups of analyses (A and B) per species were done because of differences in pot volume. Seedlings in pots with Full competition treatments (A) (without pot barriers) had access to full pot volumes, while seedlings in treatments with barriers (B) (*i.e.*, Above, Below, None) had access to a smaller pot volume and were analyzed separately. Mean values are shown (1 SE).

	Type of Competition					
	(A) Intra specific	Inter specific				
Seedling species	Full	Full		F	df	P
Acer platanoides						
MANOVA (Pillai) (all variables below)				3.02	5, 52	**0.02**
Above-ground biomass (g)	1.37 (0.21)	0.87 (0.09)		6.45	1, 56	**0.01**
Root biomass (g)	1.49 (0.20)	0.90 (0.10)		4.12	1, 56	**0.05**
Leaf Number	7.43 (0.95)	4.50 (0.75)		4.01	1, 56	0.05
Root:Shoot mass ratio	1.38 (0.10)	1.69 (0.10)		3.82	1, 56	0.06
Relative Height Growth (%) [b]	65.9 (12.1)	105.5 (14.2)		5.04	1, 56	**0.03**
Acer rubrum						
MANOVA (Pillai) (all variables below)				13.46	5, 52	**< 0.0001**
Above-ground biomass (g)	3.59 (0.27)	6.29 (0.49)		41.75	1, 56	**< 0.0001**
Root biomass (g)	3.76 (0.28)	6.57 (0.51)		36.35	1, 56	**< 0.0001**
Leaf Number	26.2 (1.65)	34.4 (2.92)		7.75	1, 56	**0.01**
Root:Shoot mass ratio	1.05 (0.05)	1.07 (0.05)		0.10	1, 56	0.75
Relative Height Growth (%) [b]	57.3 (11.2)	152.3 (20.1)		22.12	1, 56	**< 0.0001**

	(B) Above [a]	Below [a]	None [a]	F	df	P
Acer platanoides						
MANOVA (Pillai) (all variables below)				1.54	10,102	0.14
Above-ground biomass (g)	0.90 (0.18)	0.67 (0.11)	0.71 (0.10)	0.91	2, 54	0.41
Root biomass (g)	1.28 (0.18)	1.05 (0.18)	0.95 (0.10)	1.16	2, 54	0.32
Leaf Number	5.80 (0.93)	5.60 (0.96)	5.60 (0.92)	0.01	2, 54	0.99
Root:Shoot mass ratio	1.94 (0.22)	1.83 (0.20)	1.58 (0.11)	1.12	2, 54	0.33
Relative Height Growth (%) [b]	92.3 (18.2)	74.4 (16.4)	117.0 (16.9)	1.54	2, 54	0.22
Acer rubrum						
MANOVA (Pillai) (all variables below)				1.59	10,102	0.12
Above-ground biomass (g)	3.78 (0.32)	3.34 (0.31)	3.59 (0.30)	0.56	2, 54	0.58
Root biomass (g)	3.95 (0.18)	3.31 (0.28)	3.99 (0.28)	2.56	2, 54	0.09
Leaf Number	27.8 (2.17)	24.7 (1.30)	24.1 (1.49)	1.53	2, 54	0.23
Root:Shoot mass ratio	1.12 (0.06)	1.02 (0.04)	1.16 (0.05)	1.95	2, 54	0.15
Relative Height Growth (%) [b]	94.5 (19.9)	99.9 (21.3)	121.5 (17.0)	0.55	2, 54	0.58

[a] Interspecific competition

[b] Relative height growth rate (RGR) was statistically analyzed as RGR = $((\log_{10} (\text{final height} / \text{initial height})) / T)$, where T=98 days (days of experiment duration), but percentage values are shown for clarity [% growth = (((final height - initial height)/initial height) *100)].

mean values significant at the *P* < 0.05 level are shown in boldface type

Fig. 1.
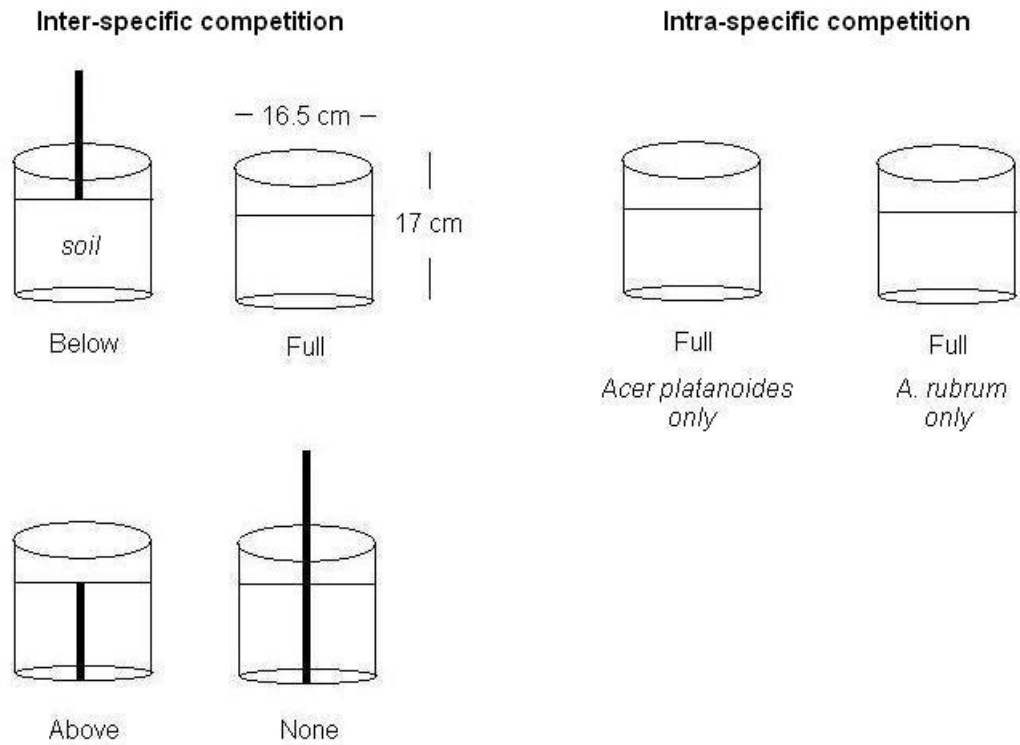
Figure 1. Illustration of plant pots and the six competition treatments used to test intra-specific and inter-specific competition (pot barriers shown as dark lines). The name of each treatment identifies the location of competition in each pot (*e.g.,* "Above" identifies that the treatment tests only for above-ground competition). All pot dimensions were 16.5 cm diameter and 17 cm tall with a volume of 3635 cm^3.

CHAPTER 3

Growth and herbivory of *Acer* seedlings in the understory of a mixed hardwood forest: comparison between an invasive and native species

Shannon L. Galbraith-Kent and Steven N. Handel

ABSTRACT

The extent and abundance of invasive plant species in eastern U.S. forests has continued to increase, often at the expense of native diversity and regeneration. *Acer platanoides* L. (Norway maple) is a shade-tolerant canopy tree that has become more important in these forests. Over a full growing season (June 2006 to June 2007), we tested the seedling growth and herbivory responses of *A. platanoides* and a native congener, *A. rubrum* L. (red maple), in a suburban forest in central New Jersey, USA.

We hypothesized that *A. rubrum* seedlings would grow best beneath a sapling community lacking an invasive tree or shrub species, while *A. platanoides* would do better beneath an invasive sapling community. However, the proportion of invasives in the understory sapling community had no effect on seedling growth, while the dominant canopy composition greatly affected *A. rubrum*, as it grew slower and to shorter heights beneath an invasive canopy (18.5 $\pm$ 1.1 cm) compared to a native canopy (24.1 $\pm$ 0.8 cm). *A. platanoides* was unaffected by the two canopy types, as seedlings under both canopies had equivalent heights. Based on the responses of the two species, current canopy composition is likely influencing regeneration dynamics (and, the future canopy) to favor the invasive *Acer*. If land management resources are constrained, we suggest periodic removal of invasive seedlings beneath a native canopy as a priority. These removals would release the native seedlings from competition with invasives in an understory where it has a greater potential to reach the canopy.

Release from natural insect enemies can be a mechanism that contributes to the success of invasive plants. Using leaves collected from *Acer* seedlings in October, we found that the mean percentage of herbivory per *A. platanoides* leaf (1.2 $\pm$ 0.3 %) did not statistically differ from *A. rubrum* (2.2 $\pm$ 0.6 %). This study cannot support the hypothesis that *A. platanoides* benefits relatively from enemy release.

KEYWORDS

Acer platanoides, Acer rubrum, seedling growth, forest understory, forest canopy, foliar herbivory, invasive species, enemy release hypothesis, Norway maple

INTRODUCTION

During the last few decades of the 20th century, eastern US forests have continued to experience changes brought upon primarily by human action (*e.g.,* increased fragmentation, deer herbivory, light levels). During this time, there have been increases in invasive plant richness and abundance, but decreases in some native species (Barton *et al.*, 2004; Bertin *et al.*, 2005; Howard *et al.*, 2004; Yates *et al.*, 2004). Not only are these species changing the current forest structure, it is likely that the future state of these forests are being impacted through negative effects on native plant regeneration for both woody (Aronson, 2007; Martin, 1999; Reinhart *et al.*, 2006a; Woods, 1993; Wyckoff & Webb, 1996) and herbaceous species (Forrest Meekins & McCarthy, 1999; Gould & Gorchov, 2000; Merriam & Feil, 2002; Miller & Gorchov, 2004; Woods, 1993). Explanations for why this is occurring include that invasive plant species may have a higher shade-tolerance (Reinhart *et al.*, 2006b; Webb *et al.*, 2000; Webster

et al., 2005), are better resource competitors than native species (Daehler, 2003; Fagan & Peart, 2004), or escape herbivory or predation from natural enemies (Keane & Crawley, 2002; Meiners, 2005; Wolfe, 2002).

In the eastern U.S., *Acer platanoides* L., Norway maple, was intentionally introduced as an ornamental tree in 1756 (Nowak & Rowntree, 1990) and has become invasive in forests across the country (Reinhart *et al.*, 2005; Wangen *et al.*, 2006; Webb & Kaunzinger, 1993). This species is very shade-tolerant, which allows it to persist in the forest understory and often colonize gaps before native species (Martin & Marks, 2006; Sipe & Bazzaz, 1995; Webster *et al.*, 2005). *A. platanoides* forms dense canopies and can alter the microenvironment beneath its canopy by increasing the soil moisture (Reinhart *et al.*, 2006a) and shade (Reinhart *et al.*, 2006b), which often facilitates the growth of conspecifics at the expense of native species (Fang, 2005; Martin, 1999; Reinhart *et al.*, 2006a; Wyckoff & Webb, 1996).

In our study, we evaluated how *A. platanoides* performed when growing with *A.rubrum* L., red maple. To understand some of the mechanisms and characteristics associated with the success of invasive species, often at the cost of native species, testing congeneric pairs in field experiments has been identified as an important method (Mack, 1996). Other than a recent dissertation (Fang, 2003), most congeneric studies with *A. platanoides* have used *A. saccharum* Marsh. (Kloeppel & Abrams, 1995; Meiners, 2005; Morrison & Mauck, 2007; Sanford *et al.*, 2003), but *A. rubrum* (L.) is the most widespread tree species in North America (Harlow *et al.*, 1996), is abundant in our region, and continues to increase in importance in the eastern U.S. (Abrams, 1998; Galbraith & Martin, 2005).

Due to their phylogenetic relationship, using congeneric species provides a good opportunity to test the enemy release hypothesis (ERH). The ERH states that an invasive species may be more successful in the invaded area than a phylogenetically

related native species, as it does not encounter natural enemies that typically suppress it, *e.g.*, through herbivory and disease (Agrawal *et al.*, 2005; Wolfe, 2002). Supporting the ERH in diverse ways, Meiners (2005) found that *A. saccharum* seeds suffered greater predation than *A. platanoides*, while Cincotta (2006) discovered that the invasive had less foliar herbivory, and that soil biota in the invaded range likely contribute to the success of *A. platanoides* (Reinhart & Callaway, 2004). However, there have been conflicting results with regards to herbivory and the ERH, with some studies in support (Cappuccino & Carpenter, 2005; Cincotta, 2006; Dietz *et al.*, 2004) and others rejecting it (Agrawal & Kotanen, 2003; Agrawal *et al.*, 2005; Morrison & Mauck, 2007). This conflict may be due to the possibility of differing effects of the ERH at each of the several stages of invasion (*i.e.,* introduction, establishment, spread) (Drake, 2003). In addition to a decreased amount of photosynthetic material, foliar herbivory can have negative consequences on plant growth (*e.g.,* increased water loss, decreased seedling recruitment) (Aldea *et al.*, 2005; Nykanen & Koricheva, 2004; Zangerl *et al.*, 2002). If *A. platanoides* does suffer less foliar herbivory through the ERH, that may be a mechanism supporting its success over *A. rubrum* and other native woody species.

In many situations, complete removal of invasive species is an unrealistic management option due to a lack of financial and logistical resources (D'Antonio & Meyerson, 2002). There may also be unintended consequences from invasive removal in the forest. A study in the region found that the removal of *A. platanoides* canopy trees did limit the recruitment of *A. platanoides* seedlings, but it was associated with a simultaneous increase in other invasive species in the understory (*e.g., Alliaria petiolata, Lonicera japonica*) (Webb *et al.*, 2001). Because of this dilemma between current management decisions and effects on the future forest composition, we asked, "if removal is unlikely, how would invasive saplings (0.3 – 2.3 m height) in understory communities affect invasive and native *Acer* seedling dynamics?" We tested seedling

growth within established, experimental communities with varying proportions of invasive

plants (0%, 25%, 50%), which served as proxies for different management outcomes.

In a forest understory, we tested the growth and herbivory of *A. rubrum* and *A.*

platanoides by planting seedlings within sapling communities that contained different

proportions of invasive plants. We hypothesized that *A. rubrum* seedlings would grow

better (a) beneath sapling communities lacking invasives and (b) with a conspecific

seedling neighbor, rather than an *A. platanoides* neighbor. Using digital leaf area

analysis, we hypothesized that the native seedlings would have more foliar herbivory.

METHODS

In this study, we tested the effects of species, sapling community treatment, type

of sapling community, and seedling plot treatment, on seedling growth and herbivory (of

Acer platanoides and *A. rubrum*) over a full growing season (June 2006 to June 2007) in

the understory of a suburban forest.

Study Site

This study was done in a post-agricultural secondary forest in the Piedmont of

central New Jersey (Somerset County, NJ) on the property of Duke Farms (1093 ha

total) (N 40˚33.8´ W 74˚25.4´). This forest (0.36 ha = 3600 m^2) was part of a larger area

enclosed by a deer fence (14 ha) and had an overstory canopy (stems > 2.5 cm dbh)

dominated by native trees similar to historical descriptions of mixed oak forests in the

area (Braun, 1950; Collins & Anderson, 1994; Monk, 1961): *Quercus alba* L. (relative

IV=19.2%), *Acer rubrum* (relative IV=16.9%), *Q. palustris* Muenchh. (relative IV=14.5%),

and *A. platanoides* (relative IV=11.9%) (S. Galbraith-Kent, *unpublished data*). The

understory was primarily composed of defined patches of the annual invasive grass,

Microstegium vimineum Trin. Camus and *Berberis thunbergii*. The soils in the forest are deep (< 200 cm to fragipan), loamy, and the primary type is Dunellen sandy loam (3 to 8% slopes), with secondary types of Lamington silt and Penn silt loam (0 to 2%, 2 to 6% slopes, respectively) (NRCS, 2007). The normal annual mean precipitation for this region of the state between 1971 and 2000 has been 126.5 cm, with a temperature of 10.5°C. During the time of this study (June 2006 to June 2007), both temperature and precipitation were above those normal values (ONJSC, 2007).

Community plot treatments

 In June 2004, locations were selected for 30 experimental woody community plots within the forest. Plots were placed in areas that did not contain *B. thunbergii* and were not in low-lying moisture depressions. The absence of *B. thunbergii* was important, so that all plots were initiated in soil chemistry conditions not directly affected by this invasive. However, most plots had 100% cover of *M. vimineum*, differing only in density of the grass. All grass was removed by hand, while litter and woody debris remained.

Fifteen plots were designated as "tree communities" and 15 plots were "shrub communities" for a total of 30 plots (Table 1). In the tree community, there were five plots per treatment type: 0% of the plants are invasive species (*i.e.,* 100% native), 25% invasive, and 50% invasive. Also, the shrub communities had this design. These tree and shrub community treatments were chosen as the native control (0% invasive), as the treatment containing equal number of plants of each species, including invasive (25% invasive) (*i.e.,* 9 plants per species), and the treatment where the plant number of the invasive species equaled the total number of all native plants (50% invasive).

We used a deWit replacement series design and kept the plant density per plot (n=36 plants/plot) the same, but varied the number of plants per species (Table 1). The density of stems was chosen in response to plant sizes, the experimental constraints of

logistics and scale, and as a measure to encourage competition, as the density was somewhat greater than in non-experimental settings. All plots (4 m x 4 m) were separated by at least 2 m and planted with the same spatial pattern of six plants per six rows with equal plant spacing (0.5 m). All plants (except *B. thunbergii*) were two-year old saplings and at least 0.3 m tall when planted. Across all plots, there were a total of 1080 tree saplings and an equal number of plants per species (n=180). When a plant died, it was replaced in October or the following April with a living plant (of the same species) new to the plot. This re-planting allowed the species proportions of treatments to remain consistent through the duration of the experiment.

The summer of 2005 set records for high temperatures and a lack of rain. To keep the plants alive during this time, we added 18.5 to 30 litres of water to each plot 4-5 times per week. For any given week, all 15 plots received the same amount of water to maintain consistency.

Sapling species selection. All native species selected were regional genotypes that had historical (Collins & Anderson, 1994; Monk, 1961) or current presence in the area (Handel & Clements, 2003) and were donated from Greenbelt Native Plant Nursery (Staten Island, NY).

At the study site in 2004, *B. thunbergii* shrubs were abundant and transplanted into the appropriate plots for this experiment. However, while *A. platanoides* was abundant as a seedling and overstorey canopy tree, there were few in the sapling size-class. Therefore, we used *A. platanoides* saplings transplanted from two regional sites (Wissahickon Watershed, Philadelphia, PA; Drew University, Madison, NJ), which were then placed into the 25% and 50% invasive tree plots. We chose saplings that were between 0.25 and 0.75 m tall, so that all plants (invasive and native) were mature understory saplings of similar size and age at the time of planting.

Seedling plot treatments

Before seedlings were planted, all *M. vimineum* and other herbaceous plants and woody seedlings were removed to make the initial vegetative cover similar (~ 0%) for all seedling plots. Any existing seedlings that were visible in these plots were removed, but all leaf litter and small woody debris remained.

This experiment had a 3x4 factorial design with four seedling plot treatments within three sapling community plots (Fig. 1). In spring 2006, seedling plots (n=4 per community plot) were constructed within each of the pre-established tree (n=15) and shrub (n=15) community plots, so that there were 120 total seedling sub-plots. The seedling plots measured 0.2m x 0.2m and were arranged in the same pattern in each community plot to help limit confounding effects of plot position (Fig. 1). The seedling densities (2 to 4 plants / $0.04m^2$) were chosen based on personal observations of seedling distributions in the forest. There were four seedling plot treatments (Table 2), with each treatment randomly designated to one of the four positions in the community plot (Fig. 1). Each seedling treatment was replicated 30 times. To maintain treatments, seedlings that died in summer of 2006 were replaced with new individuals in fall 2006.

To protect all seedling plots from small mammal herbivory, 120 cylindrical cages (0.9m height) were constructed from 20-gauge commercial poultry wire netting (with 2.54cm mesh). This type of caging has been shown not to affect the quantity of sunlight reaching seedlings (Morrison & Brown, 2004). Steel sod staples were used to secure the cages level on the forest floor.

Seedling plant material

We used seedlings of similar size and age of *A. platanoides* and *A. rubrum*. In early June 2006, *A. platanoides* seedlings were collected from within the forest and immediately transplanted into the seedling sub-plots. We used *A. rubrum* seedlings that

were greenhouse grown from seeds of naturally occurring populations within the region, since there were few *A. rubrum* seedlings in our forest site.

Light and soil conditions

The understory light environment for each plot was measured using digital photographs from a 36-mm Canon PowerShot S410 Digital Elph (4.0 megapixels) (Canon Corporation, Japan). This indirect measure was previously described (Ashton *et al.*, 2005; Engelbrecht & Herz, 2001) as a good estimate of light when compared to more direct measurements (*e.g.,* Leaf Area Index). On August 23, 2006 (at noon during partly overcast conditions), we took a photograph in the center of each plot, where the camera was leveled on a small tripod 1.5 m from the ground surface. Photographs were taken with the camera lens facing up toward the canopy and the top of the camera (containing the shutter button) facing magnetic north. For all photos, the lens was at a constant aperture (f = 2.8) and zoom and flash were disabled. The amount of open sky in the field of vision was determined using Adobe Photoshop 5.5 (Adobe Systems, San Jose, CA, USA) as previously described (Ashton *et al.*, 2005; Engelbrecht & Herz, 2001).

For each plot, we noted the dominant canopy species and described the plot as either an "invasive canopy" (*i.e., A. platanoides* as the dominant canopy species) or a "native canopy" (*i.e.,* any native species).

On June 19, 2006, soil was collected. Five cores (0-10 cm depth) were taken from each plot and combined into one sample for testing. Our samples were analyzed for chemical and textural characteristics by the Rutgers Soil Testing Laboratory (Middlesex County, New Jersey). In December 2006, we measured depth of the litter layer in each plot.

Data collection

All seedlings were tagged, heights were measured (June 2006, July 2006, June 2007), and numbers of leaves per plant were counted (June 2007). In October 2006, one leaf was randomly collected from each live seedling, placed into a plant press for drying and storage, and then later used for analyzing herbivory.

For the herbivory analysis, 180 leaves (90 per seedling species) were scanned and saved into digital format (.BMP file format) using a Hewlett-Packard 5610 All-In-One Officejet with HP Imaging Device Functions 5.3 software. The digital leaf images were then analyzed with digital software that had been downloaded from a public domain (Scion Corporation, Frederick, MD, http://www.scioncorp.com) and two measurements were made per leaf: total leaf area (cm^2) and leaf area loss (cm^2). The methodology for image analysis using the Scion Imaging software was previously described and found as more accurate in identifying leaf area loss than a leaf area meter (O'Neal *et al.*, 2002).

Statistical analysis

Seedling growth. Using a mixed effects multivariate analysis of variance (MANOVA) (PROC GLM, General Linear Model, Pillai's Trace test), we evaluated the effects of four fixed factors [*Species* (*Acer platanoides, A. rubrum*), sapling community *Plot treatment* (0%, 25%, and 50% invasive), sapling *Plot type* (shrub or tree), and *Seedling plot* treatment (four levels)] and one random factor [*Canopy dominant* (invasive or native canopy)]. The random effect and its interactions were identified with a RANDOM statement. We tested the effect of these five factors on two dependent variables: seedling height in June 2007 and relative height growth rate (from June 2006 to June 2007). Relative growth rate [RGR = ($\log_{10}$ (final height / initial height)) / T] for height was calculated using T = 365 days (length of experiment) (Beckage & Clark, 2003; George & Bazzaz, 1999). Before the MANOVA, the seedling heights were $\log_{10}$-

transformed to improve normality (Underwood, 1997) and homogeneity of sample variances was validated with Levene's test. While Wilks lambda is the most commonly used test-statistic in MANOVA, we used Pillai's Trace, which is more forgiving to violations of normality (Gotelli & Ellison, 2004). After we found two near-significant interactions in the MANOVA ($P = 0.05$, Canopy dominant * Treatment and Canopy dominant * Plot type), we sorted the data for analyses of variance (ANOVA) (PROC GLM) to clarify those patterns.

We used an ANOVA to test if mean leaf number per seedling differed between the two species. Also, in a separate ANOVA, we tested the effect of Canopy dominant on the percentage of light at the sapling level of each plot.

Using simple linear regressions (PROC REG), we tested the ability of various sapling community plot characteristics (light, soil, pre-existing conditions) to predict the mean seedling height in June 2007 (response variable). The height data were $\log_{10}$-transformed to increase normality, while predictor variables were either $\log_{10}$ or arc-sine transformed.

Seedling herbivory. We did a MANOVA similar to the one described above to test if species, sapling community plot treatment, sapling plot type, and seedling plot treatment significantly affected two dependent variables: mean area per leaf (cm^2) and relative area loss per leaf (%). We also used a simple linear regression (PROC REG) to test the ability of total mean area per leaf to predict the percent of leaf area loss (response variable). Data were $\log_{10}$ and arc-sine transformed to increase normality when appropriate.

All means and standard errors in tables and figures are original (non-transformed) units. Instead of reporting mean relative height growth rates (the largest RGR value was 0.001), we report means as percentage height increases to increase the

clarity of species trends. All analyses were done with SAS version 9.1 for Windows

(SAS Institute, Cary, NC, USA).

RESULTS

Seedling growth

From the overall MANOVA, we found that the *Acer* seedling species differed in

growth response [mean height and relative height growth rate (RGR)] during the 1

growing season period (Table 3). *Acer rubrum* had a mean height 55.4% greater than *A.*

platanoides ($F_{1, 197}$ = 34.4, P < 0.0001) and grew at a rate near three times faster than

the invasive species ($F_{1, 197}$ = 25.1, P < 0.0001) (RGR *A. platanoides* = 0.00021 +

0.000032, RGR *A. rubrum* = 0.00056 + 0.000034). Also in June 2007, *A. rubrum* (8.5 +

0.4) had more leaves per plant than the invasive (4.1 + 0.3) ($F_{1, 238}$ = 117.1, P < 0.0001).

The other significant factor in the MANOVA was Canopy dominant, as *A. rubrum*

grew 23% taller with a 46% greater RGR under a native canopy, compared to an

invasive canopy. *A. platanoides* also grew faster (61%) beneath the native canopy, but

had equivalent heights beneath the two canopies (Fig. 2). While the difference in

seedling growth rates beneath the two canopies was significant, we found the

percentages of light beneath the invasive (11.4 + 1.0%, n=6) and native canopy (10.2 +

0.8%, n=24) did not differ ($F_{1, 28}$ = 1.05, P = 0.31).

There were 2 two-way MANOVA interactions that were nearly significant (*i.e., P* =

0.05): Canopy dominant * Plot type and Canopy dominant * Plot treatment. This was not

surprising, as we saw similar Canopy dominant results when analyzing the saplings of

the community (Galbraith-Kent and Handel, Chapter 1). To evaluate if these data were

actually important, we sorted and analyzed the data with ANOVAs. There was no effect

of invasive saplings on seedling growth, as shown through the Plot treatment analysis (Fig. 3a), but Plot type (*i.e.,* shrub or tree) appeared significant (Fig. 3b). However, the positive effect of shrub plots on growth under a native canopy must be interpreted with caution, because only one (of 15) shrub plot had an invasive canopy, while there were six (of 15) tree plots with this canopy. The Plot type (shrub or tree) effects are likely due to the associated Canopy dominant effect instead (Fig. 2).

To find if there were any soil properties that could help explain these patterns and predict greater seedling growth, we did regression analyses for both *A. rubrum* and *A. platanoides*. We found that higher levels of phosphorus predicted positive seedling growth for both species (Table 4). Additionally, *A. platanoides* seedlings had greater heights in plots with higher levels of metals (copper, iron, zinc) and litter characteristics (depth, organic matter).

Seedling herbivory

In the leaf herbivory MANOVA, we found a significant difference between *Acer* species (Table 5). This difference was primarily due to a greater mean leaf area for *A. platanoides*, as the two species did not differ in loss of leaf area (Fig. 4). In the regression analyses, we found that leaves with a larger mean area for both *A. platanoides* (R^2 = 0.0074, $t_{1, 88}$ = -0.81, P = 0.42) and *A. rubrum* (R^2 = 0.0098, $t_{1, 88}$ = 0.93, P = 0.35) did not have a predictably greater percentage of mean loss per leaf. Effects of seedling plot treatments were observed in the herbivory MANOVA (Table 5), as there was significantly greater mean herbivory on seedlings in the monospecific *A. platanoides* plots (3.29 $\pm$ 1.15%) than in seedling plots with one seedling each of *A. platanoides* and *A. rubrum* (0.65 $\pm$ 0.16%) ($F_{3, 167}$ = 3.89, P = 0.01).

DISCUSSION

The structure, composition, and regeneration of forests in the eastern U.S. continue to be affected by invasive plant species (Aronson, 2007; Martin, 1999; Webster *et al.*, 2005; Wyckoff & Webb, 1996). In our study, we were interested in how understory forest communities with varying proportions of invasive tree and shrub saplings affected the seedling growth of an invasive (*Acer platanoides*) and native (*A. rubrum)* species. Additionally, we tested the enemy release hypothesis (ERH) by evaluating the amount of herbivore damage on seedling leaves.

Most studies experimentally comparing *A. platanoides* to a native congener have used *A. saccharum*, another shade-tolerant canopy tree, and found the invasive *Acer* to grow to taller heights (Meiners, 2005; Morrison & Mauck, 2007) and have greater survival (Sanford *et al.*, 2003). However, we found that *A. rubrum* grew taller, faster, and had more leaves than *A. platanoides*, but the invasive had greater area per leaf. While *A. rubrum* has a large ecological amplitude (Walters & Yawney, 1990), we did not expect it to perform better than *A. platanoides*, which often thrives in a forest understory (Reinhart *et al.*, 2006b; Wyckoff & Webb, 1996). Field studies of these two species have shown competitive displacement of *A. rubrum* by *A. platanoides* (Fang, 2003) and the suppression of *A. rubrum* recruitment in the presence of *A. platanoides* (Fang, 2005). Though both species were similar in size when planted, they were from different sources, and the *A. rubrum* seedlings likely had more than the two leaves of most *A. platanoides* seedlings. An increased leaf number might have given the native species an initial photosynthetic advantage, allowing it to grow to a greater height.

We found no impact of immediate neighbor identity and density on growth for either species. For example, whether an *A. rubrum* seedling was next to (*i.e.,* stems were between 0.10 and 0.15 m apart) an *A. platanoides* seedling or another *A. rubrum*, it had similar growth patterns. We had hypothesized that *A. rubrum* seedling growth would

be inhibited with *A. platanoides* as a neighbor, because of the potential allelopathic properties of the invasive (Sauer, 1998; Wyckoff & Webb, 1996), in addition to plants having the ability to sense competition through root neighbors (Callaway, 2002; Murphy & Dudley, 2007) and light characteristics associated with foliar shading [*e.g.,* red:far red (R:Fr) ratio] (Aphalo & Ballare, 1995). Another study in the region found decreased tree seedling growth in the presence of an invasive annual grass, [*Microstegium vimineum* (Trin.) A. Camus (Japanese stilt grass)] (Aronson, 2007). The seedlings in our study may not have been close enough to experience root competition or may have had enough resources (*e.g.,* water, light) that neighbor species identity was unimportant during our study duration.

A primary goal of this study was to discover if sapling communities containing an invasive tree (*A. platanoides*) or shrub (*Berberis thunbergii*) would inhibit the growth of *A. rubrum* seedlings. Since removing all invasive species from a site is often an unrealistic management goal (D'Antonio & Meyerson, 2002; Daehler, 2003), we tested if varying proportions would affect seedling dynamics by using treatments with an absence of invasive saplings (0% invasive), with the same number of plants per species (native and invasive) (25%), and with half of all plants being invasive (50%). However, the type of sapling treatment impacted neither *Acer* seedling species. This is contrast to the growth of native species in the sapling communities, which was negatively affected by co-occurring *A. platanoides* (Galbraith-Kent and Handel, Chapter 1). In other studies, the growth and survival of tree seedlings beneath other common shrub invaders, the honeysuckles [*Lonicera maackii* (Rupr.) Herder, *L. tatarica* L.], was significantly reduced (Gorchov & Trisel, 2003; Hartman & McCarthy, 2004; Woods, 1993), though they did not use a community framework as in our experiment. Further, a 20-yr study in a mixed hardwood forest showed that an invasive shrub, *Ligustrum sinense* Lour. (Chinese privet), could severely inhibit the herbaceous species and nearly repress all tree

regeneration. Perhaps, if our invasive sapling communities had been established for more than 2-yrs, we may have seen similar decreases in seedling growth.

One striking finding was the effect of the overstory canopy species on seedling growth. *A. rubrum* had significantly lower height and growth rate beneath an invasive canopy (*i.e., A. platanoides*) compared to a native canopy. This supports several other studies that have shown regeneration under an invasive canopy to be far less successful for *A. rubrum* (Fang, 2003) and other native species than for *A. platanoides* (Martin, 1999; Reinhart *et al.*, 2005; Wyckoff & Webb, 1996), perhaps due to greater shade beneath an invasive canopy (Reinhart *et al.*, 2006b). A study done in a forest understory in the northeastern U.S. evaluated the effect of an invasive shrub that forms dense layers, *Rhamnus frangula* L. (glossy buckthorn), and found *A. rubrum* had significantly less survival beneath high *R. frangula* cover, compared to lower invasive shrub cover (Fagan & Peart, 2004). As previously mentioned, we hypothesized that the saplings in our understory communities would affect the seedlings (because of the closer proximity), but instead found that the existing overstory canopy had the greater influence.

If land management resources are constrained, these data suggest periodic removals of invasive seedlings beneath a native canopy as a priority. Therefore, these removals (a) would not necessarily need to be done in all areas of the forest, or each year, and (b) would temporarily release *A. rubrum* and other native seedlings from invasive competition in an understory where there is greater potential to reach the canopy. In a related experiment, we suggested a similar management scheme for invasive sapling removal beneath native canopies, because native saplings grew significantly better under a native canopy over a 3-yr period (Galbraith-Kent and Handel, Chapter 1).

A. platanoides seedlings had the same height below the two canopy types, which is somewhat contrary to studies showing the invasive canopy often facilitates conspecific

growth (Reinhart *et al.*, 2005; Webb *et al.*, 2000; Wyckoff & Webb, 1996). However, another experimental study found lower *A. platanoides* growth rates in deep shade (Martin & Marks, 2006). We found the amount of light beneath the invasive and native canopies did not differ, but other light variables, such as light quantity [*i.e.,* photosynthetically active radiation (PAR)] and light quality (*i.e.,* R:Fr ratio), are lower beneath an *A. platanoides* canopy compared to a native canopy (Reinhart *et al.*, 2006b). Even with a slower growth rate in shaded understories, other studies suggest *A. platanoides* seedlings may have the ability to persist until a small gap develops and then colonize it, which has been observed for *A. saccharum* and *A. rubrum* (Marks & Gardescu, 1998; Martin & Marks, 2006; Sipe & Bazzaz, 1995; Webster *et al.*, 2005). This capability suggests *A. platanoides* could significantly alter forest composition through the seeding, sapling, and canopy layers. However, when forest restoration goals are being projected, the decision to remove *A. platanoides* canopy trees must be planned cautiously, as that action could not only increase understory native diversity, but also invasive diversity (Webb *et al.*, 2001).

While we found significant effects of the canopy dominant on *A. rubrum* growth, the interactions within the soil beneath those canopies may also be a contributing factor. In a complementary greenhouse study, *A. rubrum* had lower above- and below-ground biomass when grown in soil collected from beneath a canopy of *A. platanoides* (Galbraith-Kent and Handel, Chapter 2). Additionally, in several experiments, Leuschner has shown different root distributions and abundances of co-existing forest tree species (Buttner & Leuschner, 1994; Leuschner *et al.*, 2004), including asymmetric below-ground competition favoring an oak over a beech species (Leuschner *et al.*, 2001). The possible interaction between canopy effects, soil properties and relationships (*e.g.,* microbial communities), and rooting patterns may be contributing to the performance of native seedlings we tested.

We did examine soil properties from the sapling community plots and found both *Acer* species responded positively to phosphorus in the soil, which is an essential macronutrient needed for plant growth (Bever *et al.*, 2001; Gurevitch *et al.*, 2002) and is often utilized by *A. platanoides* better than *A. saccharum* (Kloeppel & Abrams, 1995). We also found that the invasive seedlings grew taller in plots with greater litter depths. Some have suggested that soils with a high moisture content may increase invasive growth (Howard *et al.*, 2000; Reinhart *et al.*, 2006a) at the expense of native plants. Though we did not measure soil moisture, thicker litter layers may have contributed to a moist microenvironment favoring invasive growth. Additionally, we found taller *A. platanoides* seedlings in plots with higher concentrations of calcium and metals (*i.e.,* copper, iron, zinc). Soil studies in urban areas across the world have reported increased trace metal contents (Linde *et al.*, 2007; Paterson *et al.*, 1996), including copper and zinc (Hursthouse *et al.*, 2004). If these results are generally indicative of *A. platanoides* seedling growth, the soil chemistry of urban soils could give this invasive an advantage over native competitors.

The success of some invasive plant species has been attributed to a release from natural enemies and is described as the enemy release hypothesis (ERH) (Keane & Crawley, 2002; Wolfe, 2002). The ERH suggests that introduced species will be less exposed to natural enemies (*e.g.,* predators, herbivores, parasites, pathogens), compared to their native counterparts, and will consequently achieve higher population growth rates (Drake, 2003). However, John Drake (2003) discussed that it is not well known how this release affects invasive establishment probability and reproduction, and the impact of enemy release may actually differ for each of the various stages of invasion (*i.e.,* introduction, establishment, spread). Additionally, differing types of enemy exposure (*e.g.,* soil pathogens (Reinhart and Callaway 2004), leaf herbivory) may have distinct consequences on the invasive.

In our study, we evaluated leaves of forest seedlings and did not find support for the ERH, as we found *A. platanoides* and *A. rubrum* did not differ in leaf area loss over a four-month period (July through October 2006), which supports a similar study that compared *A. platanoides* and *A. saccharum* herbivory (Morrison & Mauck, 2007). Though *A. platanoides* had a larger area per leaf than the native species, we found that leaf area had no predictive power on percent herbivory for either species, as larger leaves were not subject to greater herbivory.

Many studies have supported the ERH by showing lower relative amounts of leaf herbivory for invasive plants compared to native species (Cappuccino & Carpenter, 2005; Carpenter & Cappuccino, 2005; Cincotta, 2006; Dietz *et al.*, 2004), but others have disputed this claim (Agrawal *et al.*, 2005; Morrison & Mauck, 2007). Two studies in the same region as our experiment tested the herbivory of *A. platanoides* and *A. saccharum*, but found opposing results (Cincotta, 2006; Morrison & Mauck, 2007). Since insect populations will vary because of many factors (*e.g.,* site location, spatial and seasonality scales) within the parameters of an experimental design, these studies all offer insight into the interactions between *A. rubrum* and *A. platanoides* and may not always be comparable. Certainly, we acknowledge our study has not fully explored the ERH, as we focused only on leaves collected from one season, which were subjected just to invertebrate herbivory.

If *A. rubrum* does experience the same amount of herbivory as *A. platanoides*, which is opposite of what would be expected through the ERH (Wolfe, 2002), *A. rubrum* may have an advantage over native plant species that are subjected to greater amounts of herbivory. Over time, due to the negative consequences of leaf herbivory on plant health and growth (*e.g.,* increased water loss, lower photosynthetic rate) (Aldea *et al.*, 2005; Nykanen & Koricheva, 2004; Zangerl *et al.*, 2002), this distinction could prove beneficial to *A. rubrum* (and possibly other native species with herbivory equal to

invasives) and further increase its importance in forest communities of the eastern US (Abrams, 1998; Dodge, 1997; Galbraith & Martin, 2005).

In our study, we intentionally excluded the effects of white-tailed deer [*Odocoileus virginianus* (Boddaert)] to evaluate more direct interactions between the two *Acer* species. The increasing abundance of *O. virginianus* in the eastern U.S. has influenced the seedling layer by primarily decreasing native diversity (Rooney *et al.*, 2004; Tilghman, 1989) and survivorship (Aronson, 2007). We expect that the growth of our seedlings would have been inhibited if exposed to deer herbivory, but due to the lack of a consensus on the herbivory relationship between invasive and native plants (as described above with insect herbivory), we cannot predict if the two *Acer* species would have responded differently.

In conclusion, we tested growth and herbivory responses of *A. rubrum* and *A. platanoides* seedlings in the understory of a northeastern U.S. forest. We found that experimental understory communities, with varying proportions of invasive saplings, did not affect seedling growth. However, the canopy dominant species did affect growth, as *A. rubrum* seedlings were significantly shorter and grew slower under an invasive canopy dominated by *A. platanoides*. We found *A. platanoides* seedlings had equivalent heights beneath the two canopy types. The species responses in this experiment support similar studies, which suggest current canopy composition is likely influencing regeneration dynamics and the future canopy to favor the invasive *Acer*. We found no evidence to support the enemy release hypothesis, as *A. platanoides* and *A. rubrum* seedlings experienced the same amount of herbivory from invertebrates.

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Table 1. Experimental design of the tree and shrub sapling communities in the understory of a post-agricultural secondary forest in Somerset County, NJ. The number of plants of each species per plot are shown per treatment (0%, 25%, and 50% invasive). The number of plants per plot (n=36) was equal for each of the 30 plots.

	Plot Treatment Type (% invasive)		
	0%	25%	50%
	Tree community plots [a]		
Species	n=5	n=5	n=5
Acer platanoides	0	9	18
A. rubrum	12	9	6
Quercus rubra	12	9	6
Ulmus americana	12	9	6
Total	36	36	36
	Shrub community plots [a]		
	n=5	n=5	n=5
Berberis thunbergii	0	9	18
Ilex verticillata	12	9	6
Lindera benzoin	12	9	6
Viburnum dentatum	12	9	6
Total	36	36	36

[a] Dimensions of each plot are 4m x 4m

Table 2. Experimental design of the seedling plots within planted established sapling community plots in the understory of a post-agricultural secondary forest in Somerset County, NJ. Shown are the compositons of seedling plot treatments (n=4) and the number of those plots in each of the sapling plot treatments. Seedling plots were in both shrub (S) and tree (T) sapling community plot treatments.

| Seedling plot treatments [a] | Number of seedlings per species | | | Number of seedling plots (n) per sapling treatment | | |
| | | | | Sapling community plot treatments [b, c] | | |
	Acer platanoides	*A. rubrum*	Total per plot	0% invasive	25% invasive	50% invasive
Monospecific *Acer platanoides*	2	0	2	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)
Monospecific *A. rubrum*	0	2	2	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)
Polyspecific (2)	1	1	2	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)
Polyspecific (4)	2	2	4	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)	n=5 (S), n=5 (T)
				n=40 (total)	n=40 (total)	n=40 (total)

[a] Seedling plot dimensions = 0.2m x 0.2m

[b] Sapling plot dimensions = 4.0m x 4.0m

[c] Sapling plot treatments (n=30) = shrub (n=15) and tree (n=15) community plots. See Table 1 for planting design.

Table 3. Statistical results from the MANOVA evaluating the overall effects of species, plot treatment, seedling plot, plot type, and canopy dominant on two dependent variables [mean height of seedlings in June 2007, mean relative height growth rate (June 2006 - June 2007)].

Effect	Pillai value	F	df	P
Species [a]	0.1144	15.18	2, 235	**< 0.0001**
Plot treatment [b]	0.0334	2.01	4, 472	0.09
Plot type [c]	0.0146	1.74	2, 235	0.18
Seedling plot [d]	0.0215	0.85	6, 472	0.53
Canopy dominant [e, f]	0.0373	4.55	2, 235	**0.01**
Canopy dominant * Plot treatment	0.0393	2.36	4, 472	0.05
Canopy dominant * Plot type	0.0255	3.07	2, 235	0.05
Canopy dominant * Species	0.0013	0.15	2, 235	0.86
Plot treatment * Plot type	0.0208	1.24	4, 472	0.29
Species * Plot treatment	0.0240	1.43	4, 472	0.22
Species * Plot type	0.0008	0.10	2, 235	0.91
Species * Plot treatment * Plot type	0.0296	1.77	4, 472	0.13

[a] Species (n=2): *Acer platanoides* and *A. rubrum*

[b] Plot treatment (n=3) = 0%, 25%, and 50% invasive sapling plots

[c] Plot type (n=2) = shrub or tree sapling plot

[d] Seedling plot (n=4): monospecific *A. platanoides* (2 plants), monospecific *A. rubrum*
    (2 plants), polyspecific *A. platanoides* and *A. rubrum* (1 plant/sp.), and polyspecific (2 plants/sp.)

[e] Canopy dominant (n=2) = invasive or native canopy

[f] Canopy dominant and its interactions were random factors, while all others (Species, Plot treatment,
    Plot type, and Seedling plot) were fixed factors.

effects significant at the P < 0.05 level are shown in boldface type

Table 4. Linear regression analyses evaluating the ability of each sapling community plot (n=30) variable to significantly predict the response variable. The response (dependent) variable was the mean seedling height per plot in the last sampling period (June 2007) and was $\log_{10}$-transformed to increase normality. The predictor variables were either $\log_{10}$ or arc-sine transformed. The analyses were done for seedlings of both study species, *Acer platanoides* and *A. rubrum*.

	Seedling species			
	Acer platanoides [a]		*A. rubrum* [b]	
Plot predictor variable	R^2	*P*	R^2	*P*
Microstegium vimineum cover [c]	0.0059	0.41	0.0050	0.41
% light [d]	0.0093	0.30	0.0000	0.97
Leaf litter depth (December 2006)	0.0376 +	**0.04**	0.0021	0.59
pH	0.0198	0.13	0.0123	0.19
NO_3^- (mg/kg)	0.0296	0.06	0.0138	0.17
NH_4^+ (mg/kg)	0.0352 +	**0.04**	0.0183	0.11
P (mg/kg)	0.2330 +	**< 0.0001**	0.0362 +	**0.02**
K (mg/kg)	0.0343	0.05	0.0021	0.59
Mg (mg/kg)	0.0093	0.30	0.0094	0.26
Ca (mg/kg)	0.0387 +	**0.03**	0.0024	0.57
Cu (mg/kg)	0.2238 +	**< 0.0001**	0.0143	0.16
Mn (mg/kg)	0.0163	0.17	0.0025	0.56
Zn (mg/kg)	0.0837 +	**0.002**	0.0159	0.14
Fe (mg/kg)	0.1536 +	**< 0.0001**	0.0125	0.19
Organic Matter (%)	0.0649 +	**0.006**	0.0066	0.34

[a] degrees of freedom (*Acer platanoides*) per predictor variable = 1, 114
[b] degrees of freedom (*A. rubrum*) per predictor variable = 1, 138
[c] prior to planting of sapling plots (June 2004)
[d] % light = 100 - % overstory canopy cover
predictor variables significant at the *P* < 0.05 level are in boldface type
positive (+) signs indicate significant positive relationships between predictor and dependent variable

Table 5. Statistical results from the MANOVA evaluating the overall effects of species, plot treatment, plot type, seedling plot, and canopy dominant on two dependent variables [mean area per leaf, relative percent of leaf area loss (herbivory)]. Leaves analyzed were collected from individual seedlings in October 2006.

Effect	Pillai value	df	F	P
Species [a]	0.1230	2, 161	12.01	**< 0.0001**
Plot treatment [b]	0.0167	4, 324	0.68	0.61
Plot type [c]	0.0246	2, 161	2.03	0.13
Seedling plot [d]	0.0921	6, 324	2.61	**0.02**
Canopy dominant [e, f]	0.0263	2, 161	2.18	0.12
Canopy dominant * Plot treatment	0.0062	4, 324	0.25	0.91
Canopy dominant * Plot type	0.0063	2, 161	0.51	0.60
Canopy dominant * Species	0.0043	2, 161	0.35	0.71
Plot treatment * Plot type	0.0080	4, 324	0.32	0.86
Species * Plot treatment	0.0117	4, 324	0.48	0.75
Species * Plot type	0.0136	2, 161	1.11	0.33

[a] Species (n=2): *Acer platanoides* and *A. rubrum*

[b] Plot treatment (n=3) = 0%, 25%, and 50% invasive sapling plots

[c] Plot type (n=2) = shrub or tree sapling plot

[d] Seedling plot (n=4): monospecific *A. platanoides* (2 plants), monospecific *A. rubrum*
(2 plants), polyspecific *A. platanoides* and *A. rubrum* (1 plant/sp.), and polyspecific (2 plants/sp.)

[e] Canopy dominant (n=2) = invasive or native canopy

[f] Canopy dominant and its interactions were random factors, while all others (Species, Plot treatment, Plot type, and Seedling plot) were fixed factors.

effects significant at the $P < 0.05$ level are shown in boldface type

Fig. 1

Figure 1. An experimental understory community plot (4m x 4m) containing 36 saplings (tree or shrub), indicated by filled circles. The four seedling plots (0.2m x 0.2m) are shown as open boxes within the larger plot; each seedling treatment (n=4) was randomly assigned to one of the four locations.

Fig. 2

(a)
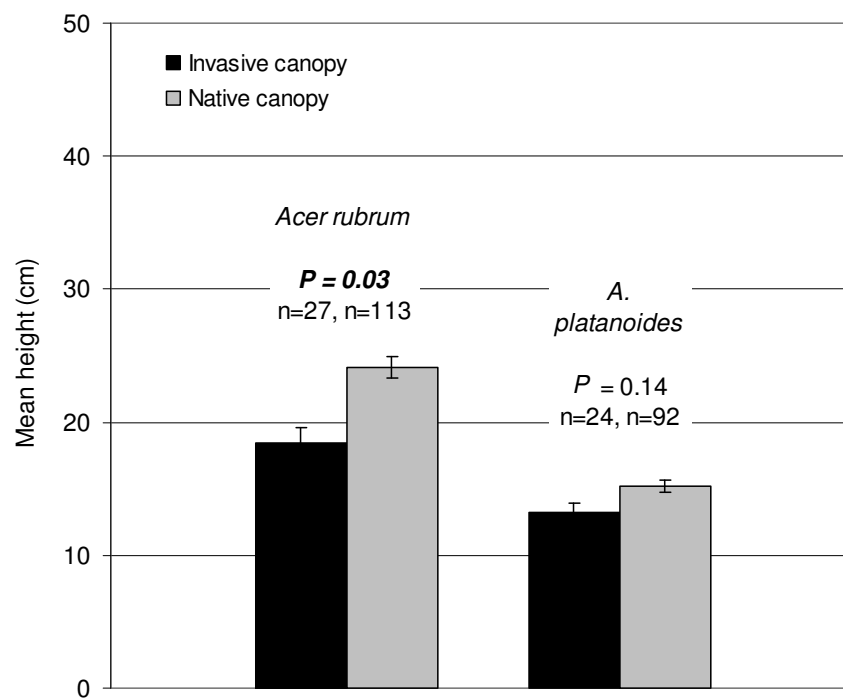
(b)
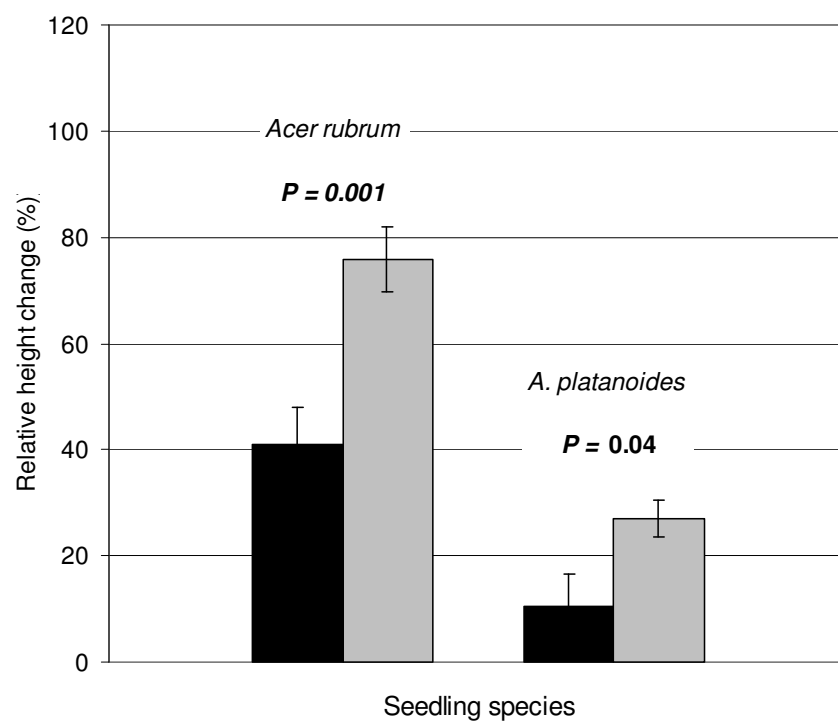
Figure 2. Analyses of variance evaluating effect of Canopy dominant on (a) seedling height (cm) (in June 2007) and (b) relative change of seedling height (%) (between June 2006 to June 2007) for each species. The invasive canopy dominant species was *Acer platanoides,* while several native species were canopy dominants, depending on the plot [including *A. rubrum, Fraxinus americana, Quercus alba, Q. palustris,* and *Pseudotsuga menziesii* (horticultural artifact on forest edge)]. Means ($\pm$ 1 SE) and number of seedlings per analysis are given.

Fig. 3

(a)

(b)
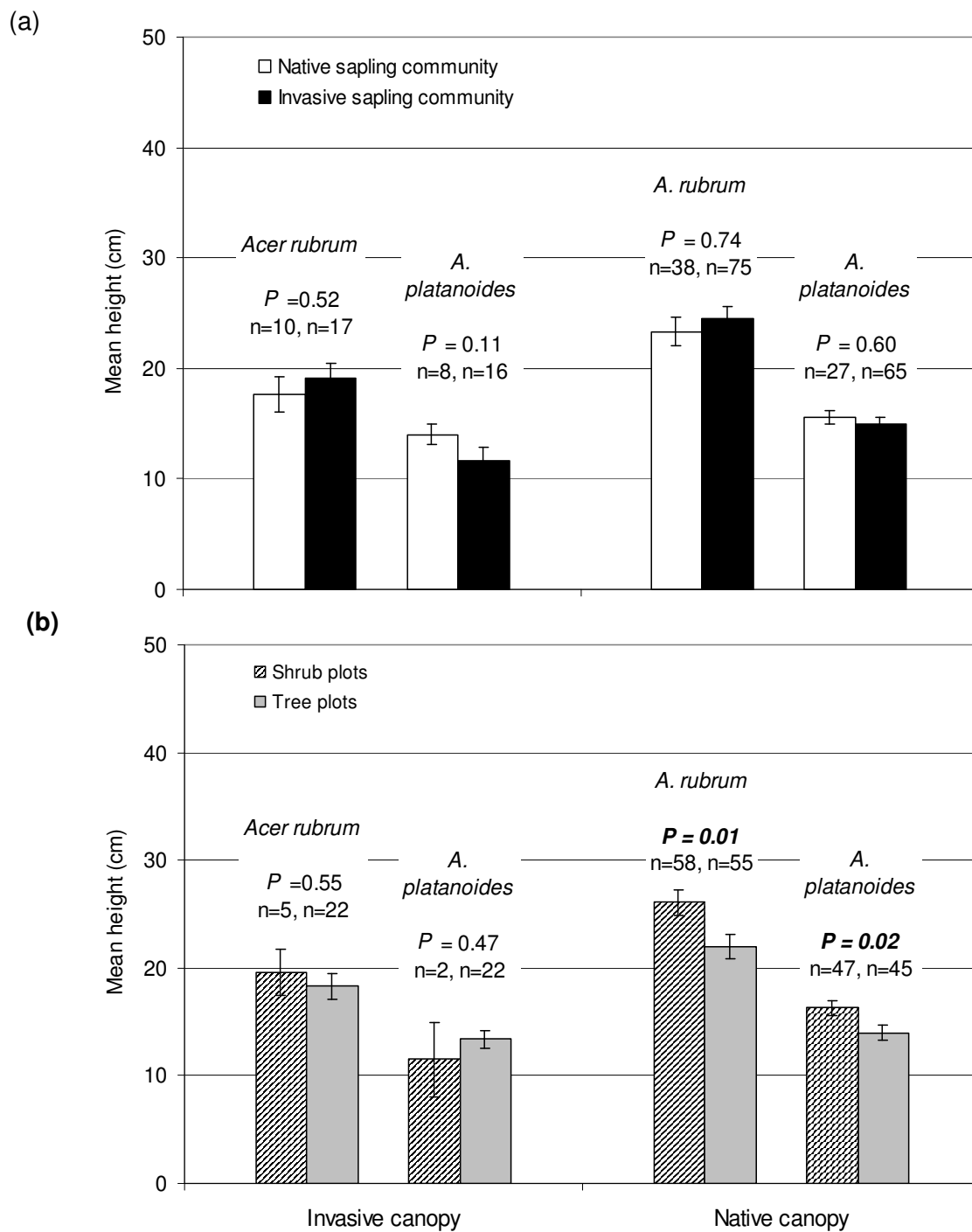
Figure 3. Statistical analyses evaluating the effects of (a) sapling community Plot

treatment (invasive or native community) and (b) Plot type (shrub or tree plot) on mean

height (June 2007), within each of the two Canopy dominant types (invasive or native

canopy). In (a), "native sapling communities" contained no invasive saplings (0%

invasive), while both communities with invasive saplings (25% and 50% invasive) were

combined as the "invasive sapling community" (see Methods for planting design). The

invasive canopy dominant species was *Acer platanoides,* while several species native to

North America were canopy dominants, depending on the plot [including *A. rubrum,*

Fraxinus americana, Quercus alba, Q. palustris, and *Pseudotsuga menziesii*

(horticultural artifact on forest edge)]. Mean values $\pm$ 1 SE, level of significance, and the

number of saplings per analysis are given.

Fig. 4
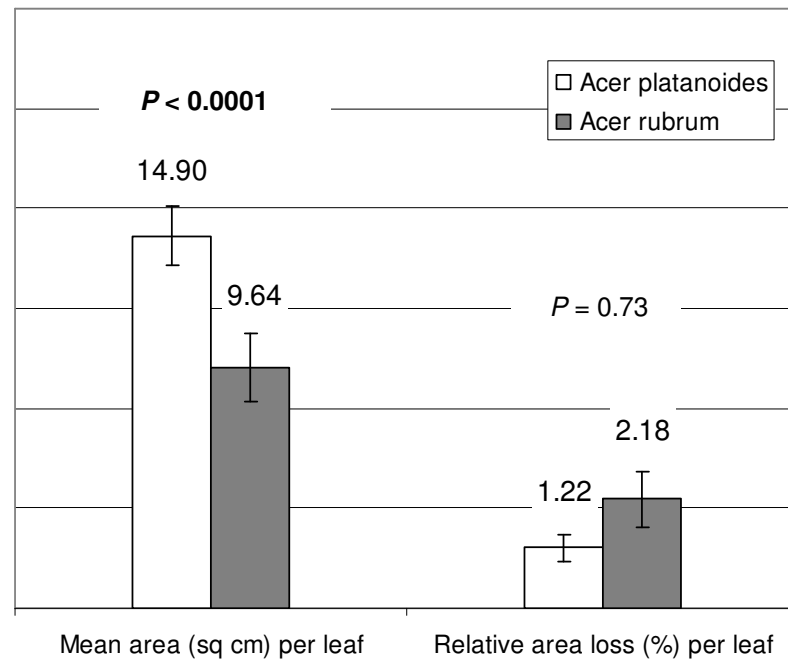
Figure 4. Mean area (cm^2) and relative area loss (%) per leaf for each seedling species, *Acer platanoides* and *A. rubrum*. Leaves analyzed (n=90 per species) were collected randomly from individual seedlings in October 2006.

CHAPTER 4

Litter decomposition dynamics of invasive and native species within experimental forest understory communities

Shannon L. Galbraith-Kent and Steven N. Handel

ABSTRACT

The changes caused by invasive plant species are usually observed through landscape vegetation patterns, but they also impact soil processes. Since removal of invasive plants is often not realistic, we were interested in how experimental understory communities (differing in proportions of invasive sapling species) affected the litter decomposition dynamics of invasive (*Acer platanoides, Berberis thunbergii*) and native woody species (*A. rubrum, Viburnum dentatum*). We found litter of both invasive species had 15% greater nitrogen content than the natives. Additionally, *B. thunbergii* had faster decomposition and a lower C:N ratio than *V. dentatum*. This is similar to other studies, which have suggested a positive-feedback loop of high nitrogen and mass loss contributing to the spread of *B. thunbergii*. Though *A. platanoides* decomposed at the same rate as *A. rubrum*, the invasive *Acer* had a 16% lower C:N ratio. This increased input and cycling of nitrogen in soil processes may be a mechanism contributing to the success of invasive plants, including *A. platanoides* and *B. thunbergii*, in eastern forests. While invasive plants can alter soils in a short time period, we did not find any impact of understory community treatment on litter decomposition. At the start of this experiment, the tree and shrub communities (containing *A. platanoides* and *B. thunbergii* saplings) had been established for 2 yrs, which may not have been enough time for soil characteristics of the communities to differentiate. There may be a legacy of impacts from invasive plant species, as they affect soil nutrients and cycling, in addition

to more obvious changes (*e.g.,* understory regeneration). This should be taken into consideration when planning for successful ecological restoration and management.

KEYWORDS

Litter decomposition, invasive species, *Acer platanoides, Berberis thunbergii*, nitrogen, Norway maple, Japanese barberry

INTRODUCTION

Accompanying the visually apparent above-ground changes in species compositions of eastern forests (Fagan & Peart, 2004; Galbraith & Martin, 2005; Webb & Kaunzinger, 1993) are more obscure changes occurring below-ground within the soil (Ehrenfeld *et al.*, 2001; Vitousek *et al.*, 1987). While these two realms have historically been considered in isolation of each other (Wardle *et al.*, 2004), they are not separate entities (Van der Putten *et al.*, 2001) and feedbacks through plant-soil linkages often control many ecosystem properties (Bever, 2003; Ehrenfeld *et al.*, 2005; Van der Putten *et al.*, 2001; Wardle *et al.*, 2004).

The decomposition of leaf litter is an important component to ecosystems, as it cycles nutrients and organic matter back to roots and soil biota (Ashton *et al.*, 2005; Gurevitch *et al.*, 2002). Invasive species typically have a higher concentration of nitrogen in leaves than native plants and are expected to decompose faster (Ehrenfeld, 2003; Vitousek *et al.*, 1987), which can cause a higher release rate into the soil than the native species (Ashton *et al.*, 2005). The presence of invasive plants can alter the soil chemistry, which can change the suite of decomposing organisms living there (Chen *et*

al., 2007; Reinhart & VandeVoort, 2006), and as result, possibly encourage more invasive species to invade (Simberloff & Von Holle, 1999). Consequently, the large-scale visual changes that are occurring as a result of invasive species introductions into deciduous forests are impacted by leaf-level processes (Ashton *et al.*, 2005; Levine *et al.*, 2003).

In the eastern U.S., the invasive shrub, *Berberis thunbergii* (Japanese barberry) began spreading in the 1920s (Silander & Klepeis, 1999) and has been found to increase soil pH, decrease litter depths (Kourtev *et al.*, 1998), decrease organic soil matter (Kourtev *et al.*, 1999), and have greater rates of litter decomposition and nitrification than native counterparts (Ehrenfeld *et al.*, 2001; Kourtev *et al.*, 1999). A positive feedback loop has been suggested for *B. thunbergii* (Ehrenfeld *et al.*, 2001): as the plant increases net nitrification in the soil, it preferentially uses the additional nitrogen for the construction of plant material leading to greater biomass and plant abundance compared to many native shrubs.

An invasive tree, *Acer platanoides* (Norway maple), continues to be a dominant species in both the understory and overstory of many U.S. forests (Reinhart *et al.*, 2005; Webb *et al.*, 2000; Webster *et al.*, 2005). Its effects on soil processes through litter decomposition are less known compared to *B. thunbergii*, but Ashton et al. (2005) found that *A. platanoides* also returned more nitrogen to the soil compared to a native congener. Mutualisms with soil biota can encourage Norway maple invasion, often at the cost of native plant regeneration (Reinhart & Callaway, 2004), and it has been suggested that allelopathy may be a possible mechanism for its success (Sauer, 1998), but recent experimental work has found otherwise (Rich, 2004).

Of the studies exploring plant-soil interactions, nearly all have been done at the population-level. A recent review found that 70% were observational and evaluated the soil differences between existing populations of invasive and native plant species

(Ehrenfeld, 2003). Of the remaining studies, 18% were experimental and most of those were mesocosm plantings done in field containers or the greenhouse. The methodology in this study used species embedded in an natural setting within relatively large experimental sapling communities (4m x 4m) containing different proportions of invasive species. Complete removal of invasive plants is often not possible due to financial and logistical constraints (D'Antonio & Meyerson, 2002; Sauer, 1998), so these understory communities served as proxies for different outcomes of invasive removal. We used litter from two invasive (*A. platanoides, B. thunbergii*) and two native *(Acer rubrum, Viburnum dentatum)* species to test differences in decomposition and carbon:nitrogen ratios in these forest understory communities. Over a 53-week period, our goals were to gather information on how these four species are both influenced (by the proportion of invasive species in the community and soil chemistry) and influence (through litter decomposition and nitrogen availability) soil dynamics in the understory of a deciduous forest.

We hypothesized that understory communities containing invasive saplings would have different soil properties such as greater nitrogen, higher pH, faster litter decomposition rates and lower C:N ratios than purely native communities. At the species level, we hypothesized that the invasive litter species would decompose faster and have lower C:N ratios.

METHODS

In this study, we evaluated the effects of time, experimental community treatments in a forest understory, and species of leaf litter, on three litter variables over a 1-yr period.

Study Site

Our study was conducted in a post-agricultural secondary forest in the Piedmont of central New Jersey (Somerset County, NJ) on the property of Duke Farms (N 40˚33.8´ W 74˚25.4´). This forest (0.36 ha = 3600 m^2) was part of a larger area enclosed by a deer fence and had an overstory canopy (stems > 2.5 cm dbh) dominated by native trees similar to historic descriptions of mixed oak forests in the area (Braun, 1950; Collins & Anderson, 1994; Monk, 1961): *Quercus alba* L. , *A. rubrum*, *Q. palustris* Muenchh, and *A. platanoides* (S. Galbraith-Kent, *unpublished data*). The understorey was primarily composed of defined patches of the annual invasive grass, *Microstegium vimineum* Trin. Camus and *Berberis thunbergii*. The soils in the forest are deep (< 200 cm to fragipan), loamy, and the primary type is Dunellen sandy loam (3 to 8% slopes), with secondary types of Lamington silt and Penn silt loam (0 to 2%, 2 to 6% slopes, respectively) (NRCS, 2007). The annual mean precipitation for this region of the state between 1971 and 2000 has been 126.5 cm, with a mean annual temperature of 10.5°C. Over the time of this study (February 2006 to February 2007), both temperature and precipitation values were above normal (ONJSC, 2007).

Plot location. In June 2004, locations were selected for 30 experimental woody community plots in the forest. Plots were placed in areas that did not contain *B. thunbergii* and were not in low-lying moisture depressions. The absence of *B. thunbergii* was important, so that all plots were initiated in soil chemistry conditions not directly affected by this invasive. However, most plots had 100% cover of *M. vimineum*, differing only in density of the grass. All of the grass was removed by hand, with the leaf litter and woody debris remaining.

Plot treatments. Fifteen plots were designated as "tree communities" and 15 plots were "shrub communities" for a total of 30 plots (Table 1). In the tree community, there were five plots per treatment type: 0% of the plants are invasive species (*i.e.,*

100% native), 25% invasive, and 50% invasive. Also, the shrub communities had this design. These community treatments were chosen as the native control (0% invasive), as the treatment containing the same number of plants for all species (25% invasive) (*i.e.,* 9 plants per species), and the treatment where the plant number of the invasive species equaled the total number of all native plants (50% invasive).

We used a deWit replacement series design and kept the plant density per plot (n=36 plants/plot) the same, but varied the number of plants per species (Table 1). The density of stems was chosen in response to plant sizes, the experimental constraints of logistics and scale, and as a measure to encourage competition. All plots (4 m x 4 m) were separated by at least 2 m and planted with the same spatial pattern of six plants per six rows with equal plant spacing (0.5 m). All plants (except *B. thunbergii*) were two-year old saplings and at least 0.3 m tall when planted. Across all plots, there were a total of 1080 tree saplings and an equal number of plants per species (n=180). When a plant died, it was replaced in October or the following April with a living plant (of the same species) new to the plot. This re-planting allowed the species proportions of treatments to remain consistent through the duration of the experiment.

The summer of 2005 set records for high temperatures and a lack of rain. To keep the plants alive during this time, we added 18.5 to 30 litres of water to each plot 4-5 times per week. For any given week, all 15 plots received the same amount of water to maintain consistency.

Sapling species selection. All native species selected were regional genotypes that had historical (Collins & Anderson, 1994; Monk, 1961) or current presence in the area (Handel & Clements, 2003) and were donated from Greenbelt Native Plant Nursery (Staten Island, NY). Each community plot contained three native species with proportions depending on treatment type (Table 1).

At the study site in 2004, *B. thunbergii* shrubs were abundant and transplanted into the appropriate plots for this experiment. However, while *A. platanoides* was abundant as a seedling and overstorey canopy tree, there were few in the sapling size-class. Therefore, we used *A. platanoides* saplings transplanted from two regional sites (Wissahickon Watershed, Philadelphia, PA; Drew University, Madison, NJ), which were then placed into the 25% and 50% invasive tree plots. We chose saplings that were between 0.25 and 0.75 m tall, so that all plants (invasive and native) were mature understorey saplings of similar size and age at the time of planting.

Experimental Design

Leaf litter of four woody species was collected from the 30 study plots during November 2005; two species were invasive (*A. platanoides, B. thunbergii*), two were native species (*A. rubrum, V.denatum*), and all four were components of the experimental plots. The species were chosen based on related taxa (*A. platanoides, A. rubrum*), presence in shrub communities (*B. thunbergii, V. dentatum*), and are often competitors in this forest type. Between November 2005 and January 2006, leaves were air-dried and weighed. Sub-samples of the initial litter were air-dried, weighed, oven-dried at 70°C, and re-weighed, to construct the necessary air-dry to oven-dry conversion for each of the four species. Leaves placed in litter bags in the field were not oven-dried, so that leaf chemistry was not altered prior to placement in the field. While some studies cut discs of leaves to maintain equal shape of the leaf matter in the bags, we used "as-is" leaves obtained from the plots to simulate field conditions, because changes in both physical and chemical characteristics of leaves can alter typical processes of litter decomposition (Gurevitch *et al.*, 2002).

The litter bags were constructed from fiberglass nylon (*i.e.,* commercial screen door material) of mesh size 1mm^2 and sealed with standard office staples; the interior

dimensions of each bag were 15 cm x 15 cm. Each bag was filled with 2.5–3.0 g of

mono-specific leaf litter. In each of the tree community plots (n=15), there were eight

total litter bags: four invasive (*A. platanoides*) and four native (*A. rubrum*). Similarly,

each shrub community plot (n=15) contained eight litter bags: four invasive (*B.

thunbergii*) and four native (*V. dentatum*). These bags were randomly assigned to one

of eight standard positions in the plot, which were separated by 0.5 m (Figure 6). These

positions were the same for all plots, because this helps prevent confounding effects

from spatial variation of bag location within the plot (Ashton *et al.*, 2005). During the

week of February 20, 2006, all of the bags were installed in the proper plots and pinned

to the mineral soil surface underneath the existing leaf litter layer.

Data collection and lab analysis. There were four harvest collection times for the

litter bags: 4 weeks (March 22, 2006), 20 weeks (July 19, 2006), 40 weeks (December 7,

2006), and 53 weeks (February 28, 2007). At each time, one litterbag per species per

plot was randomly selected. So, for example, at any one collection time, there were 15

litter bags of *A. platanoides* collected: five from each of the treatments (0%, 25%, and

50% invasive). Then, the litter was air-dried for at least 48 hours, then dried at 70˚C for

48 hours until a constant weight, and then weighed. The contents of each litter bag were

sent to the University of Nebraska-Lincoln to examine the proportions of carbon and

nitrogen using a Carbon & Nitrogen Analyzer (Costech Analytical Elemental Combustion

System 4010, Valenica, California). Due to logistical constraints, it was not possible to

analyze the samples for carbon and nitrogen before they were placed in the field.

Light and soil conditions

The understory light environment for each plot was measured using digital

photographs from a 36-mm Canon PowerShot S410 Digital Elph (4.0 megapixels)

(Canon Corporation, Japan). This indirect measure was previously described

(Engelbrecht and Herz 2001, Ashton et al. 2005) as a good estimate of light when compared to more direct measurements (*e.g.,* Leaf Area Index). On August 23, 2006 (at noon during partly overcast conditions), we took a photograph in the center of each plot, where the camera was placed parallel to the ground on a small tripod 1.5 m from the ground surface. Photographs were taken with the camera lens facing up toward the canopy and the top of the camera (containing the shutter button) facing magnetic north. For all photos, the lens was at a constant aperture (f = 2.8) and zoom and flash were disabled. The amount of open sky in the field of vision was determined using Adobe Photoshop 5.5 (Adobe Systems, San Jose, CA, USA) as previously described (Engelbrecht and Herz 2001, Ashton et al. 2005).

On June 19 (2006), soil was collected (0-10 cm depth) from each plot. Five cores were taken from each plot and combined into one sample for testing. Our samples were analyzed for chemical and textural characteristics by the Rutgers Soil Testing Laboratory (Middlesex County, New Jersey). In December 2006, we measured depth of the litter layer in each plot.

Statistical analyses

Using a multivariate analysis of variance (MANOVA), we evaluated the effects of Bag position (eight levels), Species type (two levels: invasive or native), plot Treatment (three levels), and Time (four levels), on three dependent variables: decomposition of leaf litter (mass loss), proportion of nitrogen in litter, and carbon:nitrogen ratio of litter. All independent variables were identified as fixed effects. Before the MANOVA (PROC GLM, Pillai's Trace test), the data were arc-sine square root transformed to increase normality (Underwood 1997) and homogeneity of sample variances was validated with Levene's test. While Wilks lambda is the most commonly used test-statistic in MANOVA, we used Pillai's Trace, which is more forgiving to violations of normality

(Gotelli and Ellison 2004). Analysis of variance (ANOVA) was used to analyze dependent variables once a significant effect was identified with the MANOVA.

We did a MANOVA similar to the one described above to test if the amount of light entering a plot affected the four dependent litter variables. Further, using ANOVAs, soil and light characteristics were evaluated for differences among the three plot Treatment types (0% invasive, 25%, and 50%).

All mean and standard error values in tables and figures are original (non-transformed) units. All analyses were done with SAS version 9.1 for Windows (SAS Institute, Cary, NC, USA).

RESULTS

We found that the leaf litter variables measured (leaf litter mass loss, C:N ratio, nitrogen proportion) differed over the sampling Time (between collection weeks 4, 20, 40, and 53) and by type of Species (invasive or native species). However, there was variability in addition to these factors, as the significant interaction (Time*Species) suggests other effects may also be contributing to these trends. There was no statistically important effect of community plot Treatment on overall decomposition variables (Table 2) or in any of the separate variable analyses (Fig. 1).

We evaluated how Time and Species each impacted two dependent variables (C:N ratio, leaf litter mass) and found that both were important in the differences between invasive and native species values. When grouped, the invasive species had faster decomposition and lower C:N litter ratios compared to the native species (Fig. 2). These trends were similar when we separated the analyses into the shrub and tree groups, as both native species (*Acer rubrum, Viburnum dentatum*) had significantly

greater C:N ratios over time (Fig. 3). Further illustrating this difference in allocation, there was a higher nitrogen percentage in the invasive species litter than the native species for both tree ($F_{1, 28}$ = 10.2, P = 0.0034) and shrub ($F_{1, 28}$ = 30.4, P < 0.0001) comparisons at Week 4, the first collection period (Fig. 4). But, while the invasive shrub (*Berberis thunbergii*) had significantly greater mass loss than *V. dentatum* over the 53 weeks, there was no decomposition difference between the invasive tree (*A. platanoides)* and *A. rubrum* (Fig. 3).

Of the textural and chemical soil characteristics tested, we found no significant differences among the three plot treatments (Table 3). Additionally, there was no effect of the percentage of light entering the plot on the three litter dependent variables [$F_{3, 232}$, MANOVA (Pillai) = 0.018, P = 0.24].

DISCUSSION

The impact of exotic invasive species on soil dynamics is typically not as apparent as the broad changes in vegetation patterns. With the introduction of invasive plant species, there are often increases in nitrogen availability, biomass, and litter decomposition rates (Ehrenfeld 2003). Due to changes in soil functioning and other ecological effects (*e.g.,* native diversity declines), removal of invasive species is usually desired, but is rarely a realistic management approach (D'Antonio and Meyerson 2002). Acknowledging this reality, we tested how forest understory communities with varying proportions of invasives affected decomposition dynamics by using treatments with an absence of invasive saplings (0% invasive), with the same number of plants per species (native and invasive) (25%), and with half of all plants being invasive (50%).

We were somewhat surprised to find no effect of community treatment, as purely native communities had equal decomposition rates and C:N ratios to communities with 50% invasive saplings. In a related experiment we did see these community effects, as native tree sapling growth was lower in communities containing the invasive species (Galbraith-Kent and Handel, Chapter 1). Additionally, in a 3-month time period, a greenhouse experiment found that *B. thunbergii* was able to alter the soil microbial community (Kourtev et al. 2003). That study evaluated changes directly below the invasive plants, while the litter bags we used were scattered beneath both native shrub and *B. thunbergii* individuals. While our tree and shrub communities (4m x 4m) had been established for 2 full growing seasons when the litter bags were placed, this may not have been enough time to alter decomposition processes, as we found the different treatments had similar soil characteristics (including nitrate and pH) and percentages of incoming light. While variation in soil properties (*e.g.,* soil chemistry) can occur over small scales of space and time, we designed an experiment with a relatively small study site (and the same soil series type for all plots) and similar species (taxonomically and ecologically), so that the majority of variation occurred from the effects of the 2-yr old community plot treatments.

However, we did find that invasive species had lower C:N ratios and greater litter mass loss than native species, which was also seen for most paired comparisons. This was consistent with several studies that have shown similar differences between invasive and native species (Windham 2001, Ashton et al. 2005, Chen et al. 2007), though there are invasives with opposite trends, such as a California grass (Drenovsky and Batten 2007). Decomposition rate is often positively correlated with high nitrogen content (Taylor et al. 1989, Ehrenfeld 2003), as many bacterial and fungal communities prefer nitrogen-rich litter (Melillo et al. 1982), and we found that the litter of both invasive

species (*A. platanoides* and *B. thunbergii*) had greater nitrogen percentages at Week 4 than their native counterparts (*A. rubrum* and *V. dentatum*, respectively).

In addition to the significant difference in nitrogen content, *B. thunbergii* had lost a higher percentage of litter mass than *V. dentatum* by just the fourth week of the experiment. In another study in the same region, Ehrenfeld et al. (2001) found these differences between *B. thunbergii* and native species and suggested a positive-feedback loop of high decomposition and high nitrogen likely contributes to its invasion success, as it incorporates the cycled nitrogen into additional biomass. Since it decomposes so rapidly, most of the nitrogen is released within 1 year (Ehrenfeld et al. 2001). This may encourage invasion by additional species with inducible foliar nitrate reductase (Strater and Hachtel 2000, Cassidy et al. 2004), and allow species (*e.g., B. thunbergii*) that positively respond to nitrate further dominate (Kourtev et al. 1999, Cassidy et al. 2004).

We did not find any difference in litter mass loss between *A. platanoides* and *A. rubrum*, but there was a lower C:N ratio for the invasive *Acer*. Another study comparing these two species found similar decomposition results, as well as a significantly greater nitrogen loss for *A. platanoides* (Ashton et al. 2005). Though *A. platanoides* litter may not cycle quicker to the soil than a native competitor, this invasive does contain more nitrogen and also return it faster to the soil. Perhaps similar to *B. thunbergii*, *A. platanoides* may preferentially use the cycled nitrogen to increase biomass and this may be a mechanism contributing to its success in multiple strata of eastern forests. Further, just as *B. thunbergii* has been shown to also alter soil microbial communities (Kourtev et al. 2002), a study in the western U.S. found that replacement of a dominant native species (*Populus trichocharpa*) by *A. platanoides* increased the densities of stoneflies (family Nemouridae) (Reinhart and VandeVoort 2006). It appears that *A. platanoides* may also have the capacity to alter soil nutrients and the microbial communities associated with its litter. Wider food web effects may follow here also.

As many factors affect litter decomposition (*e.g.,* soil nutrients, chemistry of plant litter, climate, decomposer communities) (Facelli and Pickett 1991), other conditions in addition to the species and time effects, could have caused the trends we observed. Though we did not observe any Eurasian earthworms at the site, they are known to facilitate the spread of invasive plant species and change soil functioning (Kourtev et al. 1999, Heneghan et al. 2006). In an Illinois oak woodland, through the combination of an invasive plant species (*Rhamnus cathartica*) and the earthworms, more than 90% of *R. cathartica* litter decomposed within 3 months (Heneghan et al. 2006). The effects of litter from invasive plant species could last after the plants are physically removed, as they can alter both the microbial communities and the soil nutrients.

In conclusion, we found temporal decomposition differences between invasive and native litter species, but not among the understory communities of varying invasive proportions. While not all invasive plant species decompose faster than natives (Ehrenfeld 2003), there may be legacy impacts of invasive plants on nutrient cycling, microbial communities, and perhaps other processes (*e.g.,* seedling regeneration). Incorporating information on litter decomposition and nutrient cycling into restoration and management decisions will promote the long-term success of an ecological restoration.

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Table 1. Experimental design of the tree and shrub sapling communities in the understory of a post-agricultural secondary forest in Somerset County, NJ. The number of plants of each species per plot are shown per treatment (0%, 25%, and 50% invasive). The number of plants per plot (n=36) was equal for each of the 30 plots.

	Plot Treatment Type (% invasive)		
	0%	25%	50%
	Tree community plots [a]		
Species	n=5	n=5	n=5
Acer platanoides	0	9	18
A. rubrum	12	9	6
Quercus rubra	12	9	6
Ulmus americana	12	9	6
Total	36	36	36
	Shrub community plots [a]		
	n=5	n=5	n=5
Berberis thunbergii	0	9	18
Ilex verticillata	12	9	6
Lindera benzoin	12	9	6
Viburnum dentatum	12	9	6
Total	36	36	36

[a] Dimensions of each plot are 4m x 4m

Table 2. Statistical results from the MANOVA evaluating the overall effects of bag position, species type, time, and plot treatment on three dependent variables (leaf litter mass loss, carbon:nitrogen ratio in leaf litter, nitrogen proportion).

Effect	Pillai value	F	df	P
Bag Position [a]	0.0762	0.77	21, 615	0.76
Species type [b]	0.0993	7.44	3, 203	**< 0.0001**
Time [c]	1.0947	39.24	9, 615	**< 0.0001**
Treatment [d]	0.0309	1.07	6, 408	0.38
Species type * Time	0.1033	2.45	9, 615	**0.01**
Species type * Treatment	0.0133	0.43	6, 408	0.86
Treatment * Time	0.0424	0.50	18, 615	0.96
Species type * Treatment * Time	0.0213	0.26	18, 615	1.00

[a] Bag positions (n=8)

[b] Species type (n=2) = invasive or native species

[c] Time (n=4) = collection times at weeks 4, 20, 40, 53

[d] Treatment (n=3) = 0%, 25%, and 50% invasive sapling plots

effects significant at the $P < 0.05$ level are shown in boldface type

Table 3. Analyses of variance evaluating the effect of sapling plot treatment (with varying invasive proportions) on various abiotic characteristics. Mean values ($\pm$ 1 SE) are shown.

Characteristic	Plot Treatment (% invasive)									F [a]	P
	0%			25%			50%				
Light [b]	11.3	$\pm$	1.5	10.9	$\pm$	1.3	9.21	$\pm$	0.7	0.83	0.45
Leaf litter depth (cm) [c]	6.0	$\pm$	0.5	5.5	$\pm$	0.4	5.6	$\pm$	0.3	0.42	0.66
Soil chemistry											
pH	4.81	$\pm$	0.12	4.58	$\pm$	0.07	4.68	$\pm$	0.07	1.75	0.19
P (mg/kg)	37.2	$\pm$	8.1	52.3	$\pm$	15.2	45.7	$\pm$	15.9	0.31	0.73
K (mg/kg)	107.0	$\pm$	13.5	95.5	$\pm$	7.1	97.8	$\pm$	6.8	0.43	0.66
Mg (mg/kg)	81.4	$\pm$	12.4	58.6	$\pm$	5.03	60.5	$\pm$	4.03	2.47	0.10
Ca (mg/kg)	459	$\pm$	104	327	$\pm$	46	392	$\pm$	57	0.80	0.46
Cu (mg/kg)	4.33	$\pm$	0.49	3.64	$\pm$	0.20	3.47	$\pm$	0.28	1.72	0.20
Mn (mg/kg)	72.2	$\pm$	8.5	55.8	$\pm$	4.1	63.5	$\pm$	5.6	1.67	0.21
Zn (mg/kg)	7.55	$\pm$	1.19	6.61	$\pm$	0.78	8.22	$\pm$	1.92	0.34	0.71
B (mg/kg)	1.27	$\pm$	0.09	1.09	$\pm$	0.05	1.34	$\pm$	0.20	0.97	0.39
Fe (mg/kg)	224	$\pm$	11	224	$\pm$	13	213	$\pm$	11	0.27	0.76
NO_3^- (mg/kg)	35.1	$\pm$	11.4	63.4	$\pm$	19.8	47.7	$\pm$	16.3	0.77	0.47
NH_4^+ (mg/kg)	39.1	$\pm$	11.2	65.0	$\pm$	18.9	51.5	$\pm$	16.0	0.68	0.51
Organic Matter (%)	4.97	$\pm$	0.34	5.88	$\pm$	0.32	6.94	$\pm$	1.21	1.73	0.20
Organic Carbon (%)	2.88	$\pm$	0.02	3.41	$\pm$	0.19	4.02	$\pm$	0.70	1.73	0.20
Soil texture											
Sand (%)	33.1	$\pm$	1.5	33.9	$\pm$	1.6	36.8	$\pm$	2.1	1.27	0.30
Silt (%)	48.3	$\pm$	1.2	47.8	$\pm$	1.6	45.1	$\pm$	1.5	1.44	0.25
Clay (%)	18.5	$\pm$	0.6	18.1	$\pm$	1.1	18.1	$\pm$	0.9	0.07	0.93

[a] df = 2, 27 per plot characteristic ANOVA; n = 10 samples per plot treatment

[b] Light is % white pixels in photo (% = 100 - canopy cover)

[c] Leaf litter depth was measured in December 2006

ANOVA tests used Type III sums of squares from SAS version 9.1 for Windows (SAS Institute, Cary, NC, USA)

Fig. 1
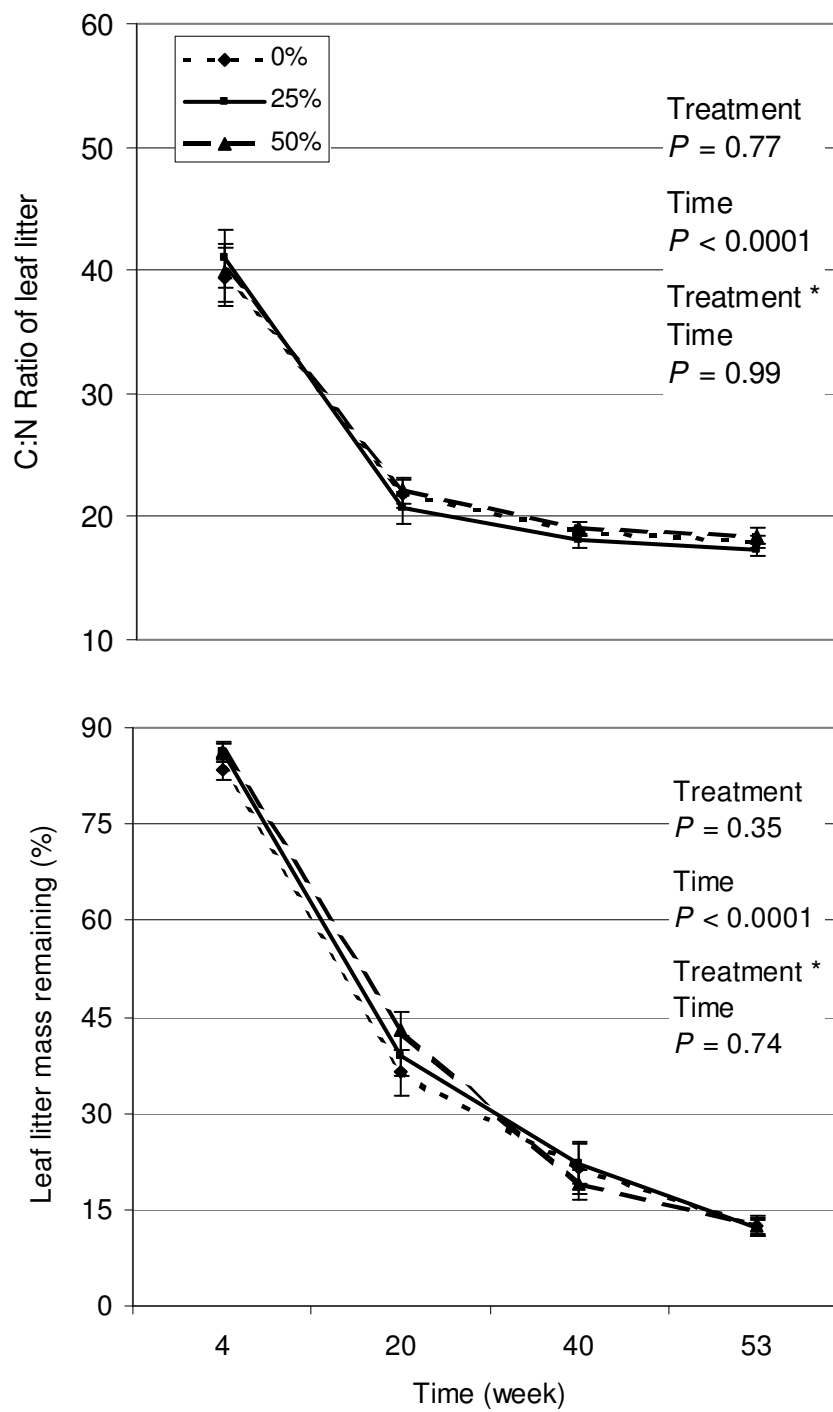
Figure 1. Statistical analyses evaluating the effect of community plot treatment (0% invasive saplings, 25%, 50%) and time on Carbon:Nitrogen ratio and percent decomposition (remaining mass) of leaf litter. The litter species included two native (*Acer rubrum, viburnum dentatum*) and two invasive (*A. platanoides, Berberis thunbergii*).   Per data point, there were n=4 species, n=10 plots, and n=5 litter bags per species. Mean values ($\pm$ 1 SE) are shown.

Fig. 2

Figure 2. Statistical analyses evaluating the effect of species type (invasive or native) and time on Carbon:Nitrogen ratio and percent decomposition (remaining mass) of leaf litter. The litter species included two native (*Acer rubrum, Viburnum dentatum*) and two invasive (*A. platanoides, Berberis thunbergii*). Per data point, there were n=2 species, n=15 plots, and n=30 litter bags. Mean values ($\pm$ 1 SE) are shown.

Fig. 3

(a)

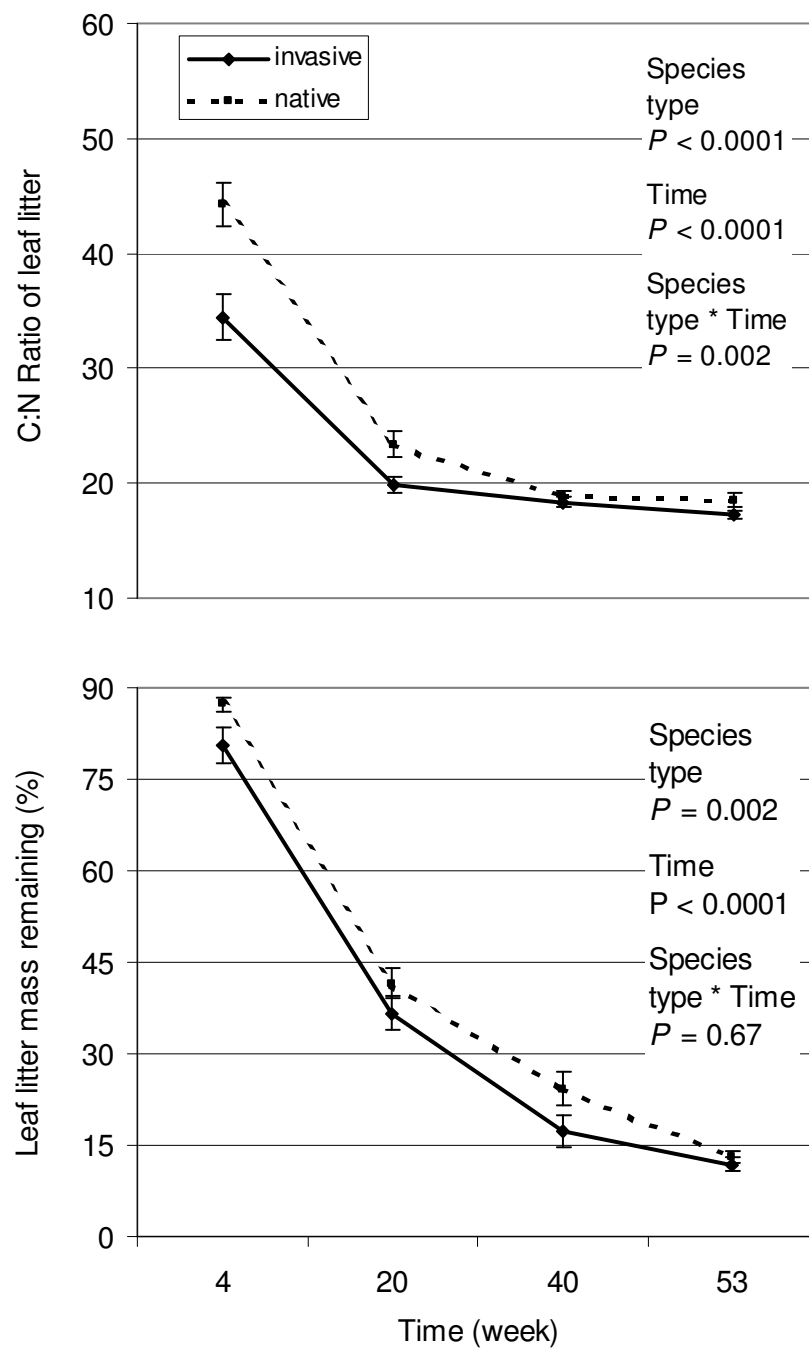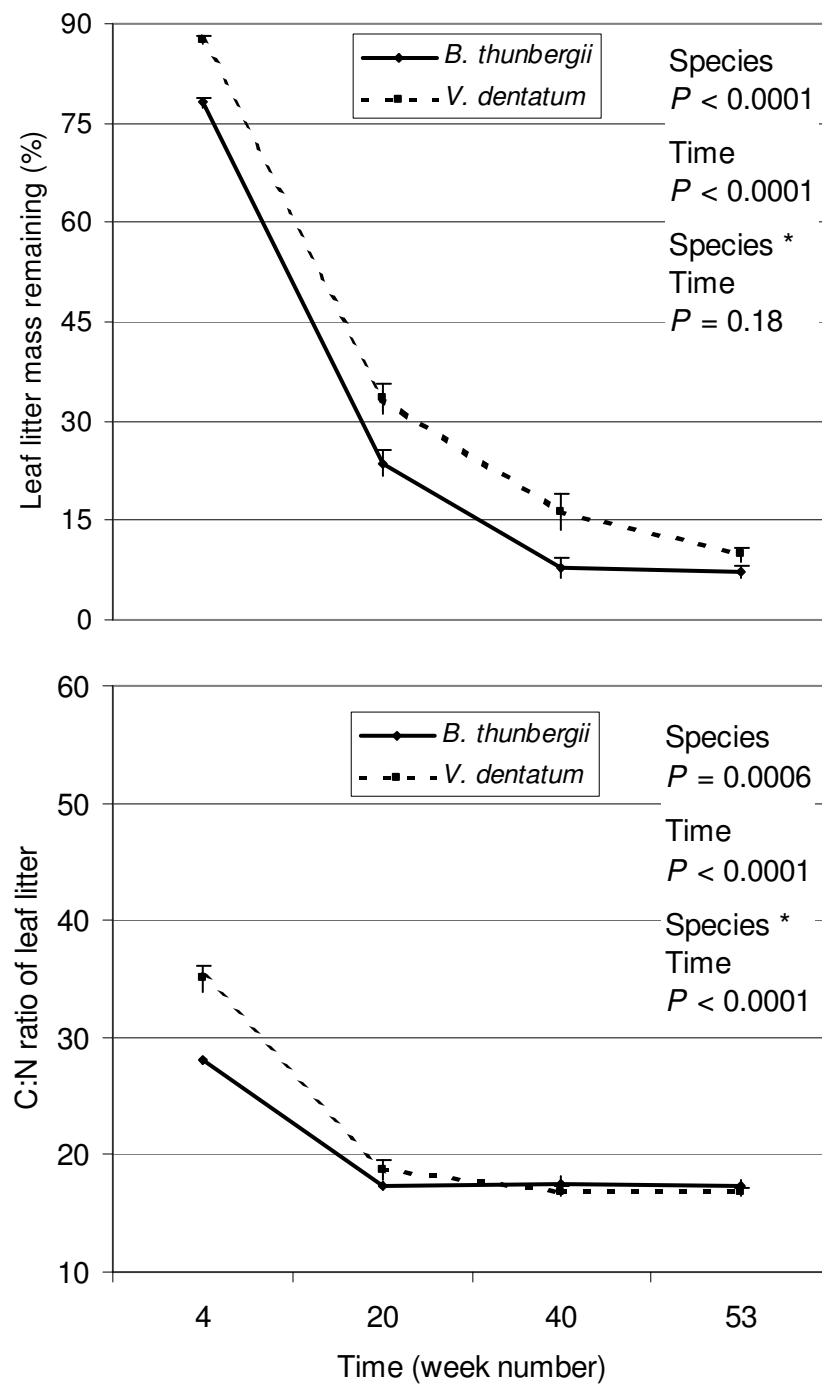Fig. 3

(b)
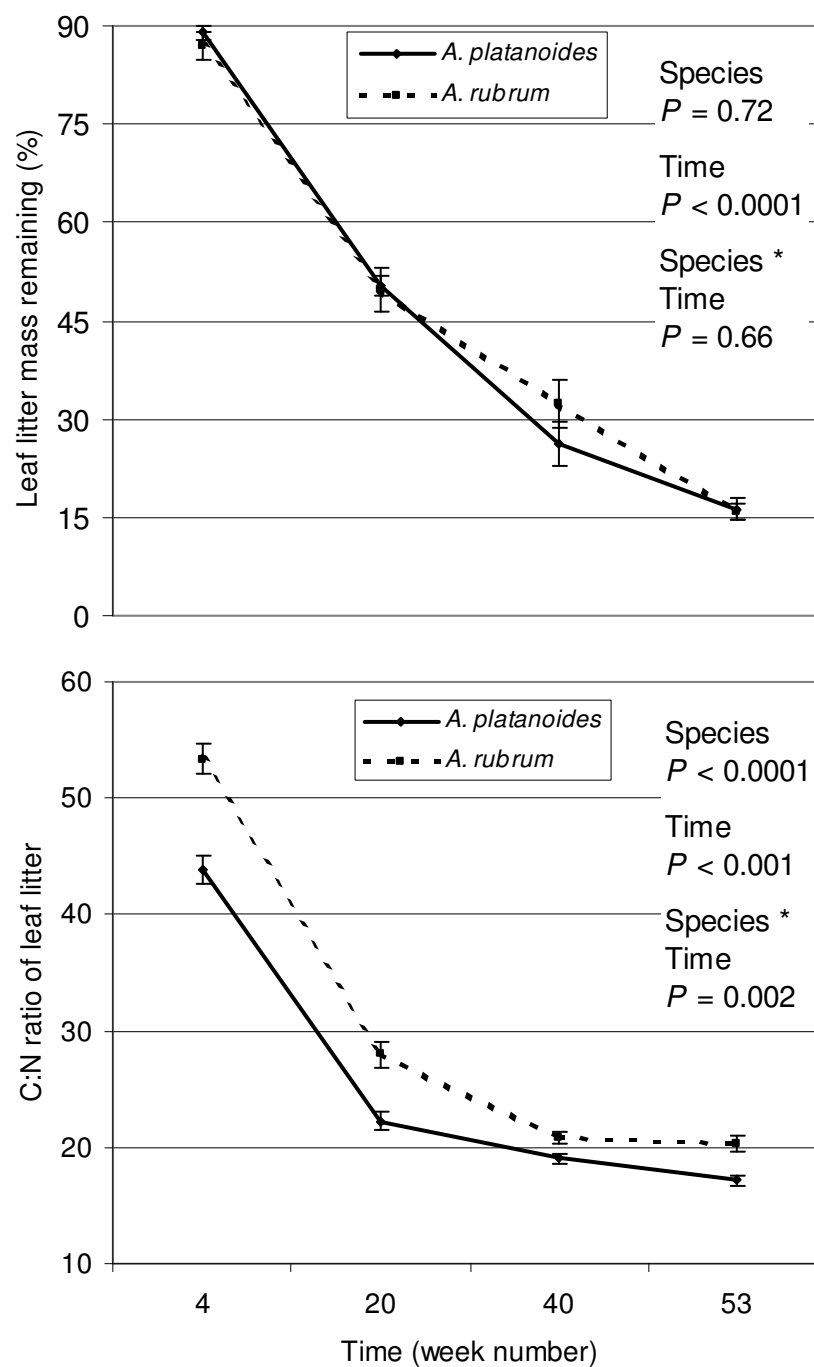
Figure 3. Statistical analyses evaluating the effect of species and time on

Carbon:Nitrogen ratio and percent decomposition (remaining mass) of leaf litter. The

litter species comparisons are shown for (a) *Berberis thunbergii* and *Viburnum dentatum*,

and (b) *Acer platanoides and A. rubrum.* Solid lines indicate the invasive species, while

the native species are dashed. Per data point, there were n=15 plots and n=15 litter

bags. Mean values ($\pm$ 1 SE) are shown.

Fig. 4

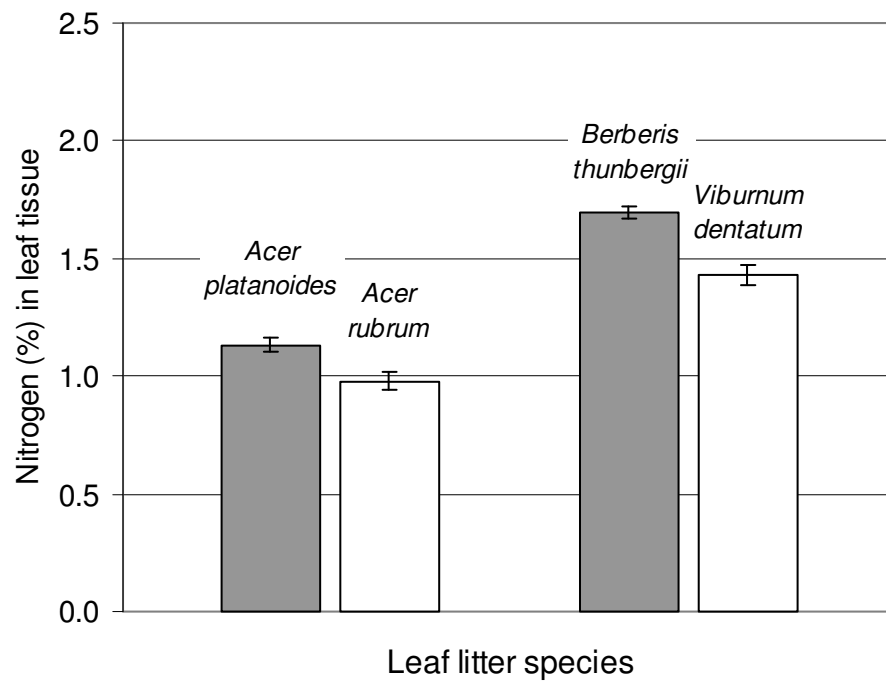Figure 4. Percent nitrogen content (± 1 SE) in leaf tissue at Week 4 of decomposition.

Invasive species are shown in gray bars, while native species are in white bars.

There were 15 samples tested per species.

CONCLUSIONS

Species present in regions other than where they evolved can become invasive and alter the structure and functioning of those invaded communities. Though the percent of these exotic species that do become invasive is relatively small (~1%), their impact on native species has been increasingly documented during the past 20 years. Unfortunately, removal of most invasive plants from eastern US forests is not a realistic option, because of the scale of invasive proliferation and the financial and logistical constraints associated with removal.

In this study, the main question I addressed was, *"What happens when invasive woody saplings cannot be completely removed from the understory of a deciduous forest?"'* Few studies have experimentally tested the impact that invasive species are having on native plants in forests at the community level. Many descriptive studies have shown the negative effects of invasive species on native plant abundance and richness, but relatively few have tested these observations. Understanding how native and invasive plant species respond under these realistic outcomes can offer us insight into the composition, structure, and functioning of our future forests.

This dissertation was built upon experimental sapling communities (4m x 4m) that were planted as tree and shrub communities in a forest understory. These communities varied in proportions of invasive plants (0%, 25%, and 50% invasive, as described in detail in Chapter 1) and were planted in summer of 2004 within the post-agricultural mixed hardwood forest located in central New Jersey (US). Overall, interspecific competition was tested using saplings in this forest (Chapter 1), as well as with seedlings in the greenhouse (Chapter 2) and forest (Chapter 3). Within those experimental communities, litter decomposition of invasive and native species was also evaluated (Chapter 4).

The two primary species tested in this study were *Acer platanoides* (Norway maple) and *A. rubrum* (red maple). *A. platanoides* is a shade-tolerant tree species that has become invasive in many areas of the US, while *A. rubrum* is also a shade-tolerant native tree species that has a large ecological amplitude and distribution range in the US. These species were chosen, because (a) they are congeners, (b) are often competitors in eastern forests, and (c) I believe *A. rubrum* might be a good species choice for restoration in forests disturbed by invasions

In CHAPTER 1, saplings were monitored for 3 growing seasons and both hypotheses were supported, as I found that native species grew significantly greater (1) in communities where *A. platanoides* was absent and (2) when beneath a native canopy. This experiment was done over 3 growing seasons and showed that *A. rubrum* grew 26% greater in a purely native community than when growing with its invasive congener. The interaction between canopy type and understory communitiy composition was striking, as it appeared that the negative effects of the invasive canopy were strong enough that the co-occurrence of invasive saplings had no impact on native growth. However, beneath a native canopy, native saplings grew significantly more in the absence of invasive saplings. Illustrating its ability to grow equally in diverse conditions, *A. platanoides* was unaffected by neither the type of understory community nor canopy species. The capability of *A. platanoides* to inhibit native saplings through understory competition and overstory canopy effects, while not affecting conspecifics, may be contributing to its success as an invader of North American forests.

Based on the interactions between *A. rubrum* and *A. platanoides* saplings, these congeners were tested together as seedlings in the greenhouse (Chapter 2) and forest (Chapter 3). To understand some of the mechanisms and characteristics associated with the success of invasive species, testing congeneric pairs has been identified as an important method. In the greenhouse (Chapter 2), I tested the effects of soil type (from

beneath invasive and native canopies) and interspecific competition on the growth of both species. The hypotheses were partially upheld, as (1) *A. rubrum* growth was inhibited in the invaded soil, while *A. platanoides* was unaffected by soil type. However, the growth results were opposite than expected, as (2) *A. rubrum* grew taller than *A. platanoides*; this was likely due to high light conditions in the greenhouse. The effect of soil on *A. rubrum* growth was important, as it had lower above-ground (32%) and below-ground (26%) biomass, and number of leaves (20%) in the invasive soil. We found the root:shoot resource allocations of *A. platanoides* depended on soil type, as it had 14% greater root:shoot mass allocation in the native soil, which may indicate a mechanism based on optimal resource partitioning contributing to its ecological success. This study showed that the impacts of *A. platanoides* on soil functioning and plant interactions must be addressed before protocols for reintroducing native tree species can be refined.

In CHAPTER 3, a complementary experiment to the greenhouse study was done within the forest understory communities. In addition, the enemy release hypothesis (ERH) was tested to find if *A. platanoides* suffered less leaf herbivory than *A. rubrum*. My hypotheses were that, (1) *A. rubrum* would grow best beneath a sapling community lacking an invasive tree or shrub species (*i.e.,* 0% invasive community) and (2) it would have less herbivory than the invasive *Acer*. Neither hypothesis was upheld, as the only factor affecting *A. rubrum* growth was the dominant canopy species. In plots where there was an invasive canopy (*i.e., A. platanoides*), *A. rubrum* seedlings grew 30% less than when beneath a native canopy. *A. platanoides* was positively correlated with several metallic soil properties, but had equivalent heights beneath the two canopy types. It appears that current canopy composition is significantly affecting regeneration dynamics at both the sapling (Chapter 1) and seedling layers (Chapter 3) to favor the invasive *Acer*. The ERH has been described as a mechanism for the success of invasive plants, as they encounter fewer enemies and, consequently, have less foliar

herbivory than their native counterparts. However, we did not find support for the ERH, as both species had equivalent leaf area loss.

While we found significant effects of the canopy dominant on both *A. rubrum* sapling and seedling growth (Chapters 1 and 3, respectively), the soil beneath those canopies may also be a contributing factor, as shown in the greenhouse experiment (Chapter 2). The possible interaction between canopy effects, soil properties and relationships (*e.g.,* microbial communities), and root patterns may all be contributing to the trends we found in the understory. A possible direction to tease out these effects could be a forest experiment using soil trenches, which would prevent canopy roots from directly affecting understory plants.

Most of the changes caused by invasive species have been observed through landscape vegetation patterns, but they also impact soil processes. In CHAPTER 4, leaf litter of two invasive (*A. platanoides, Berberis thunbergii*) and two native (*A. rubrum, Viburnum dentatum*) species was placed in the experimental forest understory communities to test the hypotheses that, (1) there would be faster decomposition rates and lower C:N ratios in the invasive sapling communities (*i.e.,* 25%, 50% invasive), and (2) invasive species litter would decompose faster and have lower C:N ratios than native litter. There were differences among species, as both invasives had lower C:N litter ratios and *B. thunbergii* litter decomposed faster than its native comparison (*V. dentatum*). This increased input and cycling of nitrogen in soil processes may be a mechanism contributing to the success of invasive plants, including *A. platanoides* and *B. thunbergii*, in eastern forests. Even though the invasive communities affected sapling growth (Chapter 1), the composition of the understory community had no impact on litter decomposition; this may have been because the communities had only been established for 2 yrs. There may be a legacy of impacts from invasive plant species, as they affect soil nutrients and cycling, in addition to more obvious changes (*e.g.,* Chapter 1 and 3).

This should be taken into consideration when planning for successful ecological restoration and management.

In this dissertation, the majority of experiments were done within experimental sapling communities that served as proxies for possible invasive management outcomes (*i.e.,* purely native community (0% invasive), 25% and 50% invasive). These treatments were specifically chosen as the native control (0% invasive), as the treatment containing the same number of plants for each species (*i.e.,* 9 plants per species) (25% invasive), and the treatment where the plant number of the invasive species equaled the total number of all native plants (50% invasive). From these experiments, there were several findings that should affect our understanding of invasive and native species interactions, the trajectory of future canopy compositions, and management decisions in eastern US forests.

After only 3 growing seasons, both an *A. platanoides* canopy and *A. platanoides* saplings had strong negative impacts on native sapling and seedling growth. The interaction between the understory community and canopy dominant was very important, as an invasive canopy had such a strong negative effect on native sapling growth that the presence of invasive saplings was irrelevant. However, beneath a native canopy, native saplings grew significantly more in the absence of invasive saplings. Even if invasive removal in the understory were only done every 2-3 yrs, this would give native saplings release from invasive competition and time to increase in growth (Chapter 1).

In two separate experiments, an invasive canopy negatively affected native seedling growth. In the greenhouse (Chapter 2), native species grew less in soil collected from beneath an invasive canopy, while seedlings in the forest were shorter below an invasive canopy compared to a native canopy (Chapter 3). While the understory and canopy types impacted native saplings and seedlings, *A. platanoides* was largely unaffected (Chapters 1, 3). However, it does appear that it has the ability to

shift resource allocation depending on soil type, which may give it a growth advantage over native species (Chapter 2). I did not find support of the ERH, as *A. platanoides* and *A. rubrum* had equivalent amounts of foliar herbivory.

In the only experiment not testing interspecific competition, leaf litter from two invasive species had lower C:N ratios than the native species. Even though some invasive species may not decompose faster than natives, their higher nitrogen content could alter soil nutrients and cycling and, perhaps, leave a legacy of invasive impact (Chapter 4).

One of the limitations of this dissertation was the lack of site replication. It would have been ideal to have these permanent experimental plots in multiple forests, but the scale of plot size and logistics involved would have made that nearly impossible. Additionally, the seedling experiments were impaired by high light conditions in the greenhouse (lack of shade-cloth) and the initial sizes of the seedlings, as I got the species from two different origins. In retrospect, I would now use seeds at the beginning of both experiments. Also, using leaves for herbivory analysis across several seasons, instead of one, would maximize exposure to various insect communities.

In conclusion, the question, "*What happens when invasive woody saplings cannot be completely removed from the understory of a deciduous forest?*", has been answered by showing that native saplings are negatively affected by the presence of invasive saplings, though an invasive canopy appears to be the primary driver in understory patterns for native species at the sapling and seedling life-stages. The effects of *A. platanoides* in the forest understory and canopy will likely make it an important component in future canopies, if episodic removals are not done. Further experimental studies testing the impacts of various invasive abundances can help us understand the interactions with native plants and what management scenarios could be employed to retain native biodiversity.

CURRICULUM VITA

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Education

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Experience

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2000 – 2002	Director, Youth and Sports Ministries, Florence Christian Church, Florence, KY
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Publications

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2005   **Galbraith, S.L.** and W.H. Martin. Three decades of overstory and species change in a mixed mesophytic forest in eastern Kentucky. Castanea 70(2): 115-128.

2007   **Galbraith-Kent, S.L.** and S.N. Handel. Lessons from an urban lakeshore restoration project in New York City. Ecological Restoration 25(2): 123-128.

2007   **Galbraith-Kent, S.L.** and S.N. Handel. Invasive *Acer platanoides* inhibits native sapling growth in understorey forest communities. Journal of Ecology *(In Press)* [Dissertation, Chapter 1].