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RESEARCH ARTICLE

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Deer and Invasive Plant Species Suppress Forest Herbaceous Communities and Canopy Tree Regeneration

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ABSTRACT: The loss of native biodiversity is a major ecological issue in human-dominated landscapes. In particular, the tree regeneration failure of deciduous forests remnants in suburban landscapes is of great concern to land managers and forestry associations. We tested the responses over two growing seasons of herbaceous plants and tree seedling survival and growth to the removal of invasive plant competition and deer herbivory. We first tested the response of understory vegetation to the removal of *Microstegium vimineum* (Japanese stiltgrass), a non-native invasive grass, and the removal of deer herbivory, via exclosures, in two forest fragments in central New Jersey. We then explored the restoration potential of planted seedlings of canopy tree dominants, *Acer rubrum, Fraxinus americana*, and *Quercus rubra*. The herbaceous community responded with an increase in species richness to the removal of *M. vimineum*. There was no response of the herbaceous community to the removal of deer herbivory, indicating that the herbaceous community will not recover rapidly from removal of these stressors alone. Survival and height growth of naturally regenerating tree seedlings increased with the removal of *M. vimineum* and the removal of deer herbivory, but these effects were not interactive. The survival and growth of planted seedlings of two tree species, *F. americana* and *Q. rubra*, were depressed by the presence of *M. vimineum*. Our results suggest that intensive management of *M. vimineum* and deer populations as well as active re-vegetation of herbaceous communities and tree seedlings are necessary to restore plant biodiversity in suburban deciduous forests.

Index terms: deciduous forests, deer herbivory, invasive plant species, *Microstegium vimineum*, restoration ecology, suburban forests, tree regeneration

INTRODUCTION

The loss of native biodiversity is of great concern in human-dominated landscapes. Specifically, forest remnants are important for the preservation of biodiversity (McKinney 2002). Small forest fragments make up the majority of forest habitats in the suburban and urban areas of the Northeastern United States (Riitters et al. 2002), and these remnants are often the only natural areas left for the conservation of biodiversity. These forests face many pressures not found in expansive, wildland forests, including intense herbivory by deer (Augustine and Frelich 1998), competition with non-native invasive plant species (Loewenstein and Loewenstein 2005), the disruption of metapopulation dynamics, decreases in air and soil quality (Pouyat and McDonnell 1991; Nowak et al. 2006), and damage by human use (Matlack 1993).

These forest fragments are in danger of losing much of their biodiversity. Overabundance of white-tailed deer (*Odocoileus virginianus* Boddaert) and the invasion of non-native plant species are considered primary stressors affecting biodiversity of forest remnants (Baiser et al. 2008; Knight et al. 2009). These factors affect current and future populations by impeding plant regeneration, eventually leading to local extirpation (Coomes et al. 2003; Rooney et al. 2004). In particular, regeneration failure of canopy trees is of concern to land managers and forestry associations.

Persistence of native diversity in the face of these stressors is influenced by factors that affect the regeneration of plant species. Deer decrease herbaceous plant species diversity and impede the survival and growth of canopy tree seedlings and saplings (Tilghman 1989; Waller and Alverson 1997). Deer may act as selective filters, enabling unpalatable, and often non-native invasive, species to dominate (Horsley et al. 2003; Rooney and Waller 2003). Germination, growth, and survival of canopy tree seedlings in temperate deciduous forests also depend on the composition and structure of the understory vegetation (George and Bazzaz 1999 a,b). Invasive plant species can alter biotic and abiotic conditions and influence overall vegetation dynamics. Studies examining the effect of plant invaders have found decreases in herbaceous and tree seedling richness, cover, and survival (Woods 1993; McCarthy 1997; Standish et al. 2001; Hartman and McCarthy 2004). Suppressed canopy tree seedlings and saplings eventually lead to inhibited canopy regeneration (Walker and Vitousek 1991; Woods 1993; de la Cretaz and Kelty 1999; Fagan and Peart 2004).

Relatively little is known about how deer and invasive species together might influence understory vegetation and the restoration of native species in suburban forest fragments. Because both deer herbivory and invasive plant species competition are generally considered major influences on forest understory vegetation, we hypothesized that these two processes will interact to have detrimental effects on the ground vegetation of isolated forest fragments. We tested the interaction of deer herbivory and competition with an invasive plant species, *Microstegium vimineum* (Trin.) A. Camus (Japanese Stiltgrass), on the recovery of understory vegetation species diversity and growth in two suburban forests in central New Jersey. We also tested the restoration success of seedlings of three dominant canopy tree species to the removal of *M. vimineum*. These experiments explore confounding factors that influence plant communities in urban forests and suggest management applications for their restoration. For management and restoration, it is imperative to know if forest remnants can develop the next generation of native plants or if constant intervention will be needed to ensure persistence. Can the diversity of suburban forests be restored with the removal of these stressors alone?

Microstegium vimineum is considered a noxious weed of 15 states in the eastern United States (Swearingen 2004). It is a shade tolerant C_4 annual grass (Horton and Neufeld 1998) native to Japan and China (Fairbrothers and Gray 1972; Kourtev et al. 1998). First introduced in Tennessee in 1919 (Barden 1987), it has become highly invasive over the past 20 years in habitats ranging from floodplains, woodland thickets, and roadsides (Fairbrothers and Gray 1972) to deeply shaded, undisturbed mesic hardwood forests (Horton and Neufeld 1998; M. Aronson, pers. observation). Forming dense carpets on the forest floor, it grows 30-100 cm tall and has shallow, fine roots that rarely extend below 3 cm in depth (Kourtev et al. 1998; M. Aronson, unpubl. data). Seeds of *M. vimineum* remain viable in the soil for at least three years (Barden 1987). It has a high competitive ability, compared with other grasses (Leicht et al. 2005), and is still spreading rapidly into new areas. In deciduous forests, *M. vimineum* changes soil processes: increasing pH, nitrification rates, and N mineralization rates (Ehrenfeld et al. 2001). It has also been shown to impede woody species regeneration (Oswalt et al. 2007). In experimental communities, *M. vimineum* decreases native plant biomass and changes the composition of native plant communities (Flory and Clay 2010a). Consequently, this species has a particularly strong ecological influence.

METHODS

Natural Regeneration and Ground Vegetation Diversity

We tested the effects of invasive species and deer herbivory on natural regeneration and growth of canopy tree seedlings and the diversity of native ground vegetation. Study sites were established in the summer of 2004 in mature secondary forests at the Hutcheson Memorial Forest (40° 29′ 55″ N, 74° 33′ 48″ W) and Duke Farms (40° 33’ 4″ N, 74° 38′ 23″ W) in Somerset County, New Jersey, located in the Piedmont physiographic region. These properties consist of a mosaic of mature primary and secondary forests, young forests, and old fields in various stages of succession. These properties are surrounded by farm fields, suburban developments, and roads. The forest fragment examined in this study at Hutcheson Memorial Forest is approximately 2.5 ha and approximately 150 years old (E.W. Stiles (deceased), ecologist, Rutgers University, pers. comm.). The forest fragment examined in this study at Duke Farms is approximately 3.9 ha and 100 years old (T. Almendinger, wildlife biologist, Duke Farms, pers. comm.). Both forests have canopies dominated by *Quercus rubra* L. and *Fraxinus americana* L. The Hutcheson Forest also supports *Q. alba* L., *Q. velutina* Lam., *Acer platanoides* L., *Prunus serotina* Ehrh., and various *Carya* Nutt. species. The canopy of the forest at Duke Farms supports *Q. alba*, *A. platanoides*, *Ulmus americana* L., and *Gymnocladus dioicus* (L.) K. Koch. The most abundant ground vegetation species at the Hutcheson Forest are *M. vimineum*, *Alliaria petiolata* (M. Bieb.) Cavara & Grande, *Eupatorium rugosum* Houtt., and *Lonicera japonica* Thunb. The most abundant ground vegetation species at Duke Farms are *M. vimineum*, *Leersia oryzoides* (L.) Sw., *E. rugosum*, *Polygonum persicaria* L., *Cardamine impatiens* L., and various *Carex* L. species. In 2004, both the Hutcheson Forest and Duke Farms supported deer populations of approximately 58-77 deer per square kilometer (E.W. Stiles (deceased), ecologist, Rutgers University, pers. comm.). However, in January 2005, after this experiment was initiated, the deer population at the Duke Farms forest site was culled to eight deer per square kilometer (T. Almendinger, wildlife biologist, Duke Farms, pers. comm.).

At each forest site, the plot design consisted of five paired plots, 6 m x 2 m, with one plot per pair fenced to exclude deer. Plots were fenced with Tenax plastic fencing, 1.2 m in height and 4.5 cm mesh size (Home Depot). Each fenced plot was topped every 0.6 meters with 0.3 m wide strips of fencing to prevent deer from jumping into the plots. Fences were designed to effectively exclude deer, but not small mammals. Plots were randomly established in areas of the forests with 100% *M. vimineum* cover. Within each paired plot, two 1 m^2 sub-plots were set up and *M. vimineum* treatments were established: one sub-plot had 100% *M. vimineum* cover and the other was reduced by hand to 0% *M. vimineum* cover. *Microstegium vimineum* seedlings were continuously removed by hand with minimal soil disturbance from the 0% treatment throughout each summer approximately every two weeks. Each pair of plots was replicated five times for a total of 10 sub-plots of 0% *M. vimineum* and 10 sub-plots of 100% cover of *M. vimineum*.

After removal of *M. vimineum*, each sub-plot was sampled for plant species composition and cover, including all woody and herbaceous species. Each tree seedling was tagged, numbered, and measured for height, and length and width of cover of the leaves. The sampling was done twice for each site in 2004 (July and September) and in 2005 (June and August).

Survival and Growth of Restored Tree Seedlings

This experiment was performed only at the Hutcheson Memorial Forest and examined the effect of *M. vimineum* on growth and survival of seedlings of three common canopy tree species. Three seedlings of *Quercus rubra*, *Fraxinus americana*, or *Acer rubrum* L. were transplanted in July 2005 with hand trowels in 0.5 m^2 monospecific paired plots, randomly assigned to one of two treatments, 100% *M. vimineum* cover or 0% *M. vimineum* cover. Seedlings were grown from seed in the spring of 2005 by Pinelands Nursery and Supply, Columbus, N.J. Ten replicates of each species and each treatment were established, for a total of 20 plots per species. All plots were fenced to exclude deer. Seedlings were surveyed for survival, height, and length and width of cover of the leaves over two growing seasons – initially in July 2005 and again in August 2005, June 2006, and August 2006. Survival and growth between July 2005 and August 2006 were analyzed. During the fall of 2006, the experiment was terminated due to a wind storm that felled large trees in the forest, taking out half of the experimental plots.

Statistical Analysis

In the regeneration experiment at the Hutcheson Forest and Duke Farms, annual survival of the July 2004 tree seedling cohort was calculated as the proportion of seedlings surviving to June 2005. Survival was analyzed for each site individually using a logit model to examine the difference in survival between exclosure treatment (removal of herbivory), invader treatment (removal of M. vimineum), and the exclosure-invader interaction (Floyd 2001). Herbaceous species richness and percent cover at the Hutcheson Forest and Duke Farms after two growing seasons (July 2004-June 2005) were analyzed for the effect of exclosure, removal of M. vimineum (invader treatment), and the exclosure-invader interaction, using a split-plot analysis of variance as a single model controlling for site. All analyses were performed in SAS version 9.1, SAS Institute, Cary, N.C.

For both the natural regeneration experiment and the seedling transplant experiment, relative growth rates were calculated for cover and height. Relative growth rates of height (HEIGHT) and cover (COVER) were calculated as HEIGHT or COVER = $(\log(y_1/y_0))/T$ (George and Bazzaz 1999b; Beckage and Clark 2003). Where y_1 is the final (August 2005 for the natural regeneration experiment and August 2006 for the seedling transplant experiment) height or cover, y_0 is the initial (June 2005 for the natural regeneration experiment and July 2005 for the seedling transplant experiment) height or cover, and T is the length of the experiment in days (George and Bazzaz 1999b; Beckage and Clark 2003). For each sub-plot or plot, a mean COVER or HEIGHT was calculated from the surviving seedlings only (Beckage and Clark 2003).

In the natural regeneration experiment, very few tree seedlings survived the first winter (eight at Hutcheson Forest and 37 at Duke Farms). Therefore, we analyzed growth rates only for the second year, from June-August 2005 for all seedlings present (n = 23 at Hutcheson Forest and n = 63 at Duke Farms). For the natural regeneration experiment, split-plot analysis of variance with least squared means (lsmeans) multiple comparisons were used to detect differences in relative growth rates of cover (COVER) and height (HEIGHT) of seedlings between exclosure treatments, invader treatments, and the exclosure-invader interaction, controlling for site. All analyses were performed in SAS version 9.1.

For the seedling transplant experiment, survival from July 2005-August 2006 was analyzed using a logit model to examine the difference in survival between the invader treatment (removal of *M. vimineum*) and species and the invader-species interaction (Floyd 2001). A X^2 test was used to analyze the effect of invader treatment on the survivorship of seedlings for each species (Walker and Vitousek 1991). Analysis of variance with post-hoc multiple comparisons of means (Tukey's HSD) and lsmeans was performed to detect differences in relative growth rates of cover and height of planted seedlings between the two removal treatments and for differences among the three canopy species. For the transplant experiment, growth rates were calculated using the measurements taken in July 2005 (y_0) and August 2006 (y_1). All analyses were performed in SAS version 9.1.

RESULTS

Natural Regeneration of Tree Seedlings and Ground Vegetation Diversity

Naturally regenerating tree seedlings at the Hutcheson Forest included *Acer rubrum*, *Fraxinus americana*, *Prunus avium* (L.) L., *P. serotina*, *Quercus alba*, and *Ulmus americana* L. Survival of the July 2004 seedling cohort to June 2005 at the Hutcheson Forest was not significantly different for exclosure treatment (Logit model; $X^2 = 0.53$; df = 1; $P = 0.470$), removal of *M. vimineum* ($X^2 = 2.21$; df = 1; $P = 0.140$), or the exclosure-invader interaction ($X^2 = 0.86$; df = 1; $P = 0.350$). However, only eight tree seedlings survived out of 20 seedlings found at the Hutcheson Forest in 2004. Naturally regenerating tree seedlings at Duke Farms included *Acer rubrum*, *Acer platanoides*, *Catalpa speciosa* (Warder) Warder ex Englem., *Fraxinus americana*, *Prunus serotina*, and *Ulmus* L. spp. At Duke Farms, 37 seedlings survived out of 125. Survival of tree seedlings at Duke Farms was 34% less ($X^2 = 11.61$; df = 1; $P < 0.001$) in the unfenced plots than the exclosures. In the presence of *M. vimineum*, survival of tree seedlings was 27% less ($X^2 = 4.03$; df = 1; $P = 0.045$) than survival of tree seedlings in the absence of *M. vimineum*. There was no effect of the exclosure-invader interaction ($X^2 = 2.26$; df = 1; $P = 0.130$) on survival of tree seedlings.

The mean cover of all seedlings at both forest sites ($n = 86$) was 36.0 ± 5.7 cm in June 2005 and 38.0 ± 4.6 cm in August 2005. The mean height of all seedlings was 10.4 ± 0.4 cm in June 2005 and 10.3 ± 0.5 cm in August 2005. There were no significant effects of exclosure, *M. vimineum* removal, or the interaction of these on the relative growth rate of cover (Table 1). The mean relative growth rate of height for seedlings in exclosures (0.0004 ± 0.0001 log(cm/cm)/d) was 38% greater than the relative growth rate of height of seedlings in the open (-0.0007 ± 0.0002 log(cm/cm)/d). The relative growth rate of height for seedlings in the absence of *M. vimineum* (0.0005 ± 0.0002 log(cm/cm)/d) was 23% greater than the growth rate of

Table 1. Results of ANOVA tests for the effects of exclosure (removal of deer herbivory), invader (removal of *M. vimineum*), and their interaction on tree seedling relative growth rates of cover (COVER) and height (HEIGHT), ground vegetation richness, and native species cover in two central New Jersey forests in June 2005. Values in bold indicate significance. AICc values: COVER = -614.9; HEIGHT = -844.6; Richness = 160.0; Native Cover = 299.5.

	COVER			HEIGHT			Richness			Native Cover		
Effect	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Exclosure	1,81.5	0.86	0.357	1,81.4	14.17	**< 0.001**	1,36	0.17	0.681	1,35	0.4	0.531
Invader	1,81.5	2.35	0.129	1,81.4	4.09	**0.046**	1,36	7.49	**<0.01**	1,35	1.74	0.196
Exclosure*Invader	1,82	2.05	0.156	1,81.9	0	0.947	1,36	1.99	0.167	1,35	1.19	0.284

height of seedlings in the presence of *M. vimineum* (-0.0007 ± 0.0002 log(cm/cm)/d). There was no interaction effect of the exclosure-invader treatments on the relative growth rate of height of tree seedlings.

Species richness of the ground vegetation at both forest sites in June 2005, one year after the experiment was initiated, ranged from 3 to 12 species per $1m^2$ sub-plot. There was no effect of exclosure on species richness, but richness significantly increased from 4.9 ± 0.4 in plots with *M. vimineum* to 6.5 ± 0.4 in plots without *M. vimineum* (Table 1). There was no effect of the exclosure-invader interaction on species richness. Cover of native species in the ground vegetation in June 2005 ranged from 62.2% to 0.4%. There were no effects of exclosure, *M. vimineum* removal, or of the interaction of exclosure-invader treatments on native species cover.

Survival and Growth of Transplanted Tree Seedlings

Survival of transplanted tree seedlings was significantly different between the two removal treatments (Logit model; X^2 = 34.63, df = 1, $P < 0.0001$) and for the tree species-invader interaction (X^2 = 16.57, $P = 0.0003$). There was a trend for better survival of *Fraxinus* and *Quercus* than *Acer* overall, but this was not significant (X^2 = 5.85, df = 2; $P = 0.054$). However, there were significant differences between the invader treatments within species. Survival of *Fraxinus* grown in the presence of *M. vimineum* was reduced 67% (X^2 = 22.50, df = 1, $P < 0.001$), compared to survival without *M. vimineum* (Figure 1). Survival of *Quercus* was reduced 84% (X^2 = 29.43, df = 1, $P < 0.001$) in *M. vimineum* plots than in plots with no *M. vimineum*. Survival of *Acer* grown in the presence or absence of *M. vimineum* did not differ (X^2 = 0.28, df = 1, $P = 0.598$).

The mean cover of the transplanted seedlings was 187.8 ± 10.4 cm in July 2005 and 359.1 ± 31.2 cm in August 2006. The overall model of the ANOVA of the relative growth rate of cover (COVER) was significant (F = 10.17, df = 5, 35, $P < 0.001$). There were significant effects of species and invader treatments on COVER of seedlings (Table 2). There was no significant interaction effect of the species-invader treatments. The COVER of all seedlings combined grown with *M. vimineum* was less than the COVER of seedlings grown without *M. vimineum* (Table 2). The COVER of *Quercus* was decreased ($P = 0.003$) in the presence of *M. vimineum* (Figure 2). Although there was a trend of reduced COVER of *Fraxinus* in the presence of *M. vimineum*, this was not a significant reduction ($P = 0.068$). *Acer* did not show significant differences ($P = 0.76$) in COVER when grown with or without *M. vimineum*. Among species, regardless of treatment, *Fraxinus* COVER was greater ($P < 0.05$) than *Acer* and *Quercus*.

The mean height of the transplanted seedlings was 21.0 ± 0.5 cm in July 2005 and 25.3 ± 1.1 cm in August 2006. For the relative growth rate of height (HEIGHT),

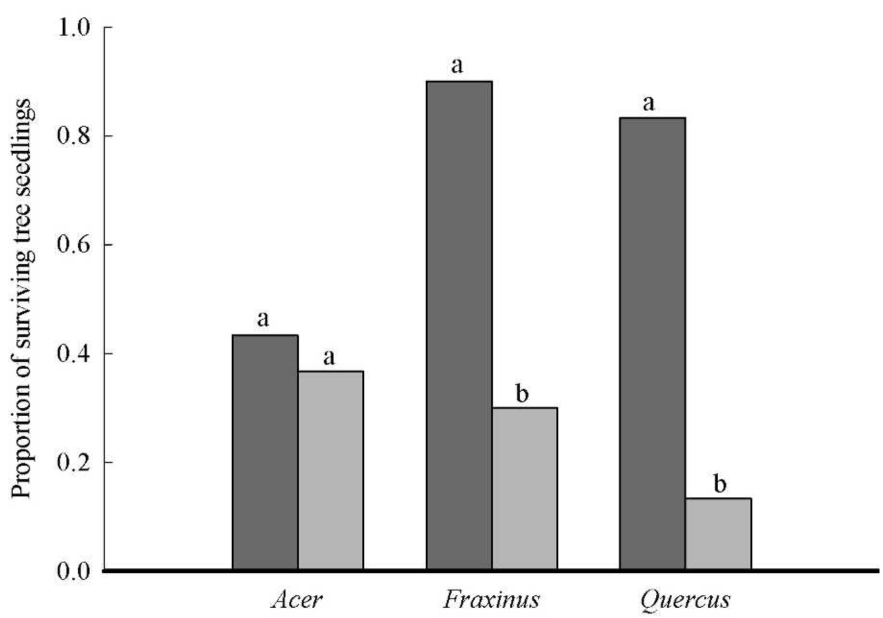

Figure 1. Proportion of surviving transplanted tree seedlings grown with (light grey bars) and without (dark grey bars) *M. vimineum*. Bars with different letters within species are significantly different ($P < 0.05$); *Acer* (X^2 = 0.28, df = 1, $P = 0.598$), *Fraxinus* (X^2 = 22.50, df = 1, $P < 0.001$), *Quercus* (X^2 = 29.43, df = 1, $P < 0.001$).

Table 2. Results of the ANOVA tests and Tukey's HSD multiple comparisons on the effects of species and invader (removal of *M. vimineum*) on the relative growth rates of cover (COVER) and height (HEIGHT) for three species transplanted at the Hutcheson Memorial Forest, New Jersey. Different letters within levels indicate significant differences at P < 0.05. n = 41; *Acer* n = 12; *Fraxinus* n = 18; *Quercus* n = 11.

Effect	df	COVER *F*	COVER *P*	HEIGHT *F*	HEIGHT *P*
Species	2, 37	18.63	**< 0.001**	18.49	**< 0.001**
Invader	1, 38	23.99	**< 0.001**	31.51	**< 0.001**
Species*Invader	2, 34	3.02	0.06	6.68	**0.003**
	Levels	Mean±SE log(cm/cm)/d		Mean±SE log(cm/cm)/d	
	Acer	-0.0001±0.0003[a]		-0.0001±0.0001[a]	
Species	*Fraxinus*	0.0009±0.0002[b]		0.0003±0.0001[b]	
	Quercus	-0.0004±0.0003[a]		-0.0001±0.0002[a]	
Invader	0% *M. vimineum*	0.0005±0.0002[a]		0.0002±0.0001[a]	
	100% *M. vimineum*	-0.0003±0.0003[b]		-0.0002±0.0002[b]	

the ANOVA model was significant (F = 10.91, df = 5, 35, $P < 0.001$). There were significant effects of species, invader, and the species-invader interaction on HEIGHT. *Fraxinus* had significantly greater HEIGHT than *Quercus* and *Acer* (Table 2). Overall, the presence of *M. vimineum* reduced the relative growth rates of tree seedlings. The presence of *M. vimineum* decreased ($P < 0.001$) the HEIGHT of *Quercus* (Figure 3). *Acer* ($P = 0.60$) and *Fraxinus* ($P = 0.29$) did not show significant differences in HEIGHT when grown with or without *M. vimineum*.

DISCUSSION

Restoration success of eastern deciduous forests depends on multiple factors. We demonstrated that white-tailed deer herbivory and competition with *M. vimineum* influenced herbaceous forest diversity and regeneration of dominant canopy tree species. The early recovery and restoration of eastern deciduous forests may be impossible without management of both these stressors.

The exclusion of deer and removal of *M. vimineum* increased the survivorship of naturally regenerating tree seedlings. Seedling survivorship has been found to be strongly affected by white-tailed deer herbivory, and species often exhibit differential survivorship according to their tolerance of herbivory (Boerner and Brinkman 1996). For example, in an Ohio deciduous forest, *Fraxinus americana* and *Quercus* species survived between 5-7 months, while survivorship of *Acer saccharum* Marsh. and *Ulmus americana* was approximately 1 year (Boerner and Brinkman 1996). While we were unable to examine individual species survivorship of naturally regenerating seedlings due to the small sample size, *Fraxinus americana* dominated the seedling pool at Duke Farms and survivorship of seedlings was much reduced after one year. Differential survivorship of canopy tree seedlings, even under low deer densities, may well affect the composition of future canopy dominants.

Growth of naturally regenerating canopy tree seedlings was significantly reduced by deer herbivory and *M. vimineum*. Our data indicate that an invaded forest community may not recover if only the influence of deer herbivory is removed. Other research has shown that decreasing deer alone will not allow a forest to recover, particularly when an invasive plant has come to dominate the understory (de la Cretaz and Kelty 2002; Coomes et al. 2003; Knight et al. 2009). There may be several ecological processes interfering with recovery of canopy tree regeneration after reduction of intense deer herbivory. First, resources left by the extirpation of palatable species may be now used by unpalatable species (Coomes et al. 2003). Second, species may be unable to reestablish due to the loss of

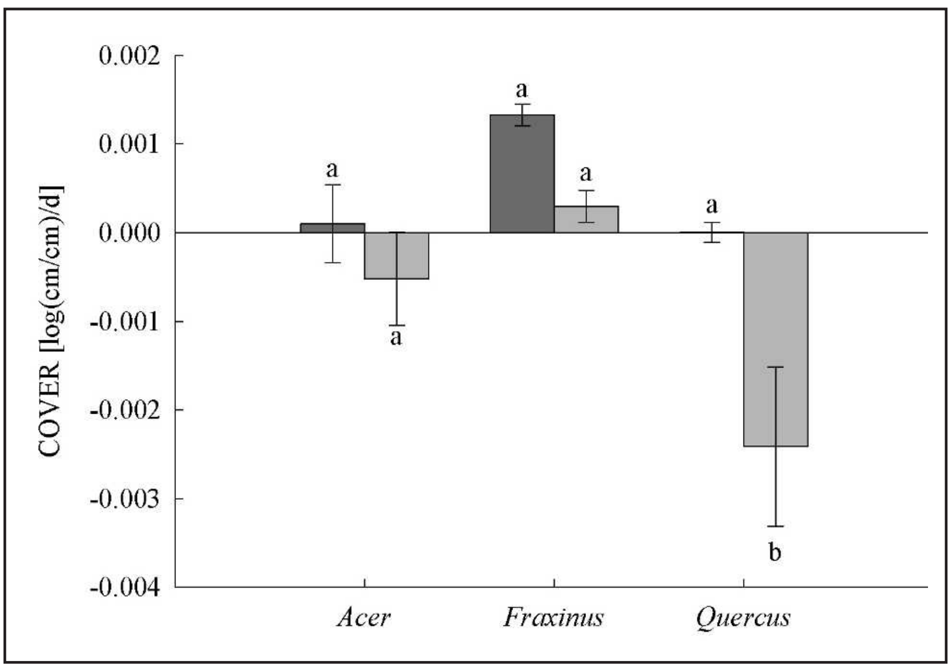

Figure 2. Average (±SE) relative growth rate of cover (COVER) of *Acer rubrum*, *Fraxinus americana*, and *Quercus rubra* seedlings grown in the presence (light grey bars) and absence (dark grey bars) of *M. vimineum*. Bars with different letters within species are significantly different (*P* < 0.05).

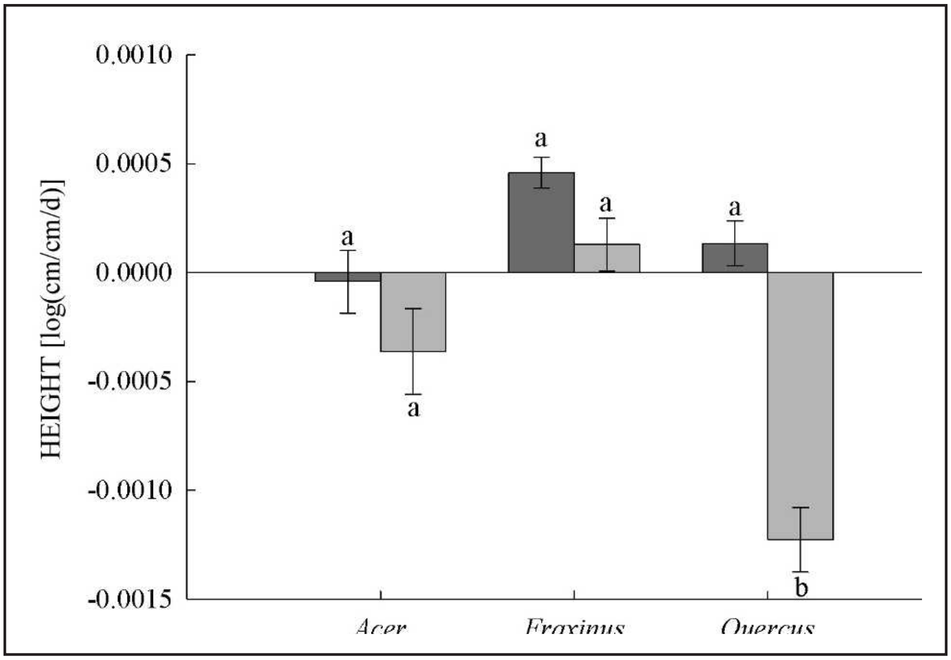

Figure 3. Average (±SE) relative growth rate of height (HEIGHT) of *Acer rubrum, Fraxinus americana*, and *Quercus rubra* seedlings grown in the presence (light grey bars) and absence (dark grey bars) of *M. vimineum*. Bars with different letters within species are significantly different ($P < 0.05$).

local seed sources (Coomes et al. 2003), or seed banks may be exhausted from years of overbrowsing. Third, overbrowsing promotes new successional trajectories dominated by tolerant or unpalatable plant species (Coomes et al. 2003; Horsley et al. 2003; Rooney and Waller 2003). These new successional trajectories, maintained by years of overbrowsing, may not be easily reversed. Fourth, overbrowsing has been shown to change soil properties and fauna, causing long-term alterations to forest ecosystem processes (Wardle et al. 2001; Coomes et al. 2003; Rooney and Waller 2003). Finally, introduction of exotic plants and animals also inhibit forest recovery (Coomes et al. 2003).

Although we did not find an effect of deer herbivory on ground vegetation diversity, it is well established that the overabundance of deer causes declines in overall understory diversity and cover (Tilghman 1989; Waller and Alverson 1997; Augustine and Frelich 1998; Horsley et al. 2003; Côte et al. 2004; Rooney et al. 2004; Knight et al. 2009). In an old growth forest in Pennsylvania, declines in understory species diversity between 1929 and 1995 were attributed to increased deer herbivory (Rooney and Dress 1997). We may not have observed an effect of deer herbivory on herbaceous diversity in the forests studied here because these forests had already been severely degraded by deer herbivory over 25 years (Aronson 2007), eliminating many sensitive species. Herbaceous species dominant in our plots, such as *Eupatorium rugosum* and *Phytolacca americana* L., appear to be tolerant of deer herbivory (M. Aronson, pers. observation) and, as we demonstrated, would be expected to have a greater response to the removal of *M. vimineum* than to deer herbivory.

Microstegium vimineum is expected to have a particularly strong influence on the herbaceous layer of hardwood forests because of its dense populations and closed canopy. Our results support previous studies that the removal of *M. vimineum* may increase the productivity of resident herbaceous plant species (Flory et al. 2007; Flory 2010). In experimental plant communities, *M. vimineum* significantly reduced native species diversity and biomass (Flory and Clay 2010a). While we expected greater recovery of the native plant community with the removal of *M. vimineum*, such recovery could have been compromised on our sites due to a lack of native seed bank resulting from the long history of intense deer herbivory. The herbaceous layer may need more time than the length of this study (two growing seasons) to recover from long-term deer herbivory and non-native species invasions. Natural recovery of the herbaceous layer in degraded forests such as these may not be feasible and may require active re-vegetation.

Forest restoration is affected by invasive plant species. We found decreases in survival and growth rates of transplanted seedlings in the presence of *M. vimineum*. This has not been previously shown with preexisting populations of *M. vimineum* and very few studies have shown the effects of herbaceous non-native plants on tree regeneration (McCarthy 1997). However, Flory and Clay (2010b) recently showed differential germination of tree species in experimental populations of *M. vimineum*. The germination of some tree species, particularly those with small seeds, was reduced with the presence of *M. vimineum*. Few other studies have shown the detrimental effects of invasive non-native herbs on regeneration of tree species. For example, *Alliaria petiolata*, another non-native invasive plant in eastern deciduous forests, also out-competes native tree seedlings and herbaceous species (Meekins and McCarthy 1999), often by disrupting mutualistic mycorrhizal associations with tree seedlings (Stinson et al. 2006).

Competition for light and water are probably the most important factors influencing tree seedling performance in forest communities (Walker and Vitousek 1991; Davis et al. 1998; Standish et al. 2001; Gorchov and Trisel 2003). We did not examine light levels and soil water content, but *M. vimineum* apparently competes for both of these resources with tree seedlings. First, *M. vimineum* is taller than and has greater abundance than tree seedlings, resulting in greater leaf area. Second, *M. vimineum* appears to be a better competitor for soil moisture. In 2005, there was a summer drought, but *M. vimineum* survived longer than the tree seedlings in both our experiments. Further studies are needed to confirm the resources most important for competition. Flory and Clay (2010b) suggested that competition for light was one of the primary factors affecting tree regeneration in *M. vimineum* experimental communities.

Although *M. vimineum* is an annual species, it decreased the growth rate and survival of two tree species, *F. americana* and *Q. rubra*. These results, in addition to the results of the natural regeneration experiment, suggest a future change in community structure and canopy composition. In this way, *M. vimineum* and other invasive herbaceous species may act as keystone species, influencing the population dynamics of canopy trees. The understory herbaceous stratum can act as an "ecological filter" and differentially affect the regeneration of canopy tree seedlings (George and Bazzaz 1999 a,b). When non-native invasive species act as ecological filters, they may favor the most shade tolerant tree species. Those species most tolerant to invasive species are expected to dominate the community (Standish et al. 2001; Fagan and Peart 2004). Of six tree seedling species in northeastern United States forests, *Fraxinus americana* exhibited the greatest survival in competition with *Lonicera maackii* (Rupr.) Herder (Hartman and McCarthy 2004). In another study, *Acer saccharum* displayed greatest survival when released from competition from *L. maackii* (Gorchov and Trisel 2003). The presence of non-native plant species alters the canopy seedling pool, which could alter canopy composition.

We suggest forest recovery is unlikely without management of white-tailed deer and *M. vimineum*. Recently, Knight et al. (2009) showed that deer and non-native plant species may synergistically reduce native plant diversity. While it is still undocumented if there is an interactive effect of white-tailed deer herbivory and invasive species competition on forest understory diversity and tree-regeneration, it is clear that both are important influences. Unless intensive management programs are instituted to control deer and non-native invasive species, regeneration of the native dominant canopy tree species is unlikely in hardwood forests such as these. Active restoration efforts, such as planting tree seedlings, fencing of seedlings, and the removal of non-native competitors, are needed to ensure the survival and growth of future canopy dominants. Although we did not experimentally address the survival and growth of specific native herbaceous species with invaders, it is clear that the rich herbaceous flora of the northeastern United States forests will not completely recover with simply the removal of deer and invasive competitors. Active revegetation is also needed to restore native herbaceous communities. Without management, the understory of the future forest may be dominated by *M. vimineum* and other unpalatable non-native invasive herbs, such as *Alliaria petiolata*, and shrubs, such as *Berberis thunbergii* DC. With the death of the mature canopy species, those species with greatest tolerance to deer herbivory and *M. vimineum* competition, such as *Ailanthus altissima* (Mill.) Swingle (Aronson 2007), may eventually dominate the canopy, forming a new, and less diverse, forest.

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