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HISTORICAL LEGACIES, COMPETITION AND DISPERSAL CONTROL
PATTERNS OF INVASION BY A NON-NATIVE GRASS, *MICROSTEGIUM*
VIMINEUM TRIN. (A. CAMUS).

by

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ABSTRACT OF THE DISSERTATION

Historical legacies, competition and dispersal control patterns of invasion by a non-native grass, *Microstegium vimineum* Trin. (A. Camus).

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Biological invasions can be controlled by a number of factors, and the importance of these factors for individual species can change depending on the spatial scale under consideration. Furthermore, the long-term legacies of past land use may be among the major factors structuring contemporary communities. This study was designed to merge these two lines of thought by observing the processes influencing invasion success of an exotic grass species, *Microstegium vimineum*. Plots within twenty hardwood forest stands of different ages (40 years old to >100 years) were surveyed in central New Jersey for the presence and abundance of this species, and the data was analyzed using simple, multiple

linear and logistic regressions, as well as regression trees. At the stand scale, *M. vimineum* abundance was influenced by age, slope, shrub cover and forest connectivity, with far more predictable responses in younger stands than in old. On the plot scale, forest age and prior use were again the dominant influences on abundance of the invasive. Invasion in old forests was most promoted by thinner canopy cover, while younger stands were most influenced by soil type and distance to forest edge. Further studies along dispersal corridors (streams and trails) in these stands consistently showed more invasion in younger stands than older, but also found the intensity of invasion to be higher along such corridors than through areas without them. Observation of isolated patches confirmed that seed dispersal is mostly short-range without dispersal conduits, with most seeds germinating less than a meter from their parent patch boundaries. Finally, an experimental study of the role of understory shrub cover and litter depth on seed germination and seedling growth showed that shade from shrubs strongly limits survival and growth. Seeds also need to be in contact with mineral soil to establish, but otherwise litter depth does not influence growth. These studies demonstrate that the establishment and spread of this invasive species is affected by complex hierarchies of factors that differ in stands with different land use histories. Land managers can use these differences to design targeted control programs that are more effective and stand-specific.

DEDICATION

To the Sourlands and their residents, past and present.

And to Katie, for her joy and patience.

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INTRODUCTION

Interest in invasion ecology, both from scientists and the general public, has never been higher, and a large amount of active research is continuing to broaden our understanding of how and why invasions occur. Much early research focused on the traits that confer invasive tendencies to species (Daehler 1998, Sakai *et al.* 2001), or on the other side of the coin, that determine community invasibility (Prieur-Richard & Lavorel 2000, Stohlgren *et al.* 2002, Levine *et al.* 2003). But over the last few years, there has been an increasing awareness of the common determinants of a species' success, whether native or exotic. All species are responding to the same selective pressures, despite the multitude of strategies they possess in response to those pressures (Davis *et al.* 2000, Gilbert & Lechowicz 2005). This helps to explain why invasive species tend to be concentrated in areas where native species are also diverse; these tend to be habitats rich in resources (Stohlgren *et al.* 1999, Levine 2000). Another recurring theme is the connection between invasion and habitat disturbance, as many invasives are highly tolerant of disturbance (Hobbs & Huenneke 1992, Davis *et al.* 2005). Since habitats around the world are undergoing an increasing amount of disturbance from natural and especially anthropogenic forces, it is not surprising to find invasion increasing in those habitats as well. Yet another area of recently growing research, particularly in plant ecology, is the influence of land use legacies on contemporary communities. Researchers have been documenting the incredible persistence of historical effects, in some cases up to thousands of years in duration (Beach 1998, Dambrine *et al.* 2007). This influence is likely due to the synthetic nature of land use history; it affects many aspects of community formation, from propagule pressure to edaphic resource availability and

beyond (Gerhardt and Foster 2002, Hall *et al.* 2002, Verheyen *et al.* 2003). As a result, legacy effects are excellent candidates for deepening our understanding of invasion processes, and yet their potential is just beginning to be explored (Figueroa *et al.* 2004, Lundgren *et al.* 2004).

Another recent conceptual expansion in invasion ecology and ecology more generally, is the idea of hierarchical constraints on community interactions (Diez and Pulliam 2007). This is simply the understanding that the relative strength of limiting factors for a species may be altered in the presence versus absence of another limiting factor (Belyea and Lancaster 1999, De'Ath and Fabricius 2000). For instance, shade and light limitation may be primary determinants of the success of an invader, but the question is moot without first having appropriate dispersal corridors and vectors in place to introduce propagules. Thus, our modeling of species distributions for management efforts must take into account the contingent structure of these limiting influences in order to be most effective (Huston 2004).

As a variable with many contingent components, land use legacy entails many covariates that affect plant community development, but increasing the temporal scale of observations also allows detection of establishment windows that might be closed under current conditions. This phenomenon may partly explain the invasion of plants into mature communities, in that they were introduced to the landscape when conditions were more favorable for establishment (higher light, better dispersal opportunities, etc.) and have persisted there as the community matured around them. This was recently postulated as a main driver for current distributions of an invasive shrub, *Berberis*

thunbergii (DeGasperis and Motzkin 2007). The applicability of this concept to an invasive annual, which can not expand through clonal growth and is reliant on disturbance, has yet to be tested, though. Of course, disturbance effects have not remained static over the previous decades either, and may be a more important promoter of continued invasion than historical legacies for some species (MacDougall and Turkington 2005). This study attempts to integrate these disparate lines of thought through a case study of an invasive annual grass in eastern North America, *Microstegium vimineum*.

Previous work on *M. vimineum* has demonstrated that the species is most often constrained by low light conditions, but can tolerate a wide range of soil and climate conditions (Horton and Neufeld 1998, Gibson *et al.* 2002, Cole and Weltzin 2004). Its initial appearance in a region is always along dispersal corridors, and thus it is presumably disturbance or dispersal limited in the early stages of invasion (Scholz and Byfield 2000, Peskin 2005). Yet it is one of the relatively small group of species that regularly invades less-anthropogenically-disturbed habitats, making it a concern for biodiversity loss and homogenization (Leicht *et al.* 2005, Belote and Weltzin 2006). Its current range is the entire eastern portion of the United States, from the Southeast north to Massachusetts, and it is beginning to filter across the Appalachians and into the Ohio valley. Its arrival in North America (first record was 1919; Fairbrothers and Gray 1972) is also coincidental with the beginnings of large-scale farm abandonment and subsequent afforestation in the eastern states. Thus it is an ideal species for studying the role of historical legacies in invasion, since it is encountering a wide range of forest ages as it expands its range.

The first two chapters of this study are observations of *M. vimineum* populations at almost 1250 plots in twenty forest stands of varying ages and disturbance histories in a very heterogeneous landscape in western New Jersey. Chapter 1 considers the data from the largest scale, that of the entire landscape, by comparing populations across the stands. I hypothesized that smaller, younger stands with a higher proportion of edge habitat would contain higher densities of the invasive species than older and larger stands. Also, those forest stands with greater connectivity to other forests, both now and in the past, were expected to have lower levels of invasion, due to greater buffering from the introduction of propagules. In addition to these properties of the stands themselves, several variables were estimated for each stand by averaging the values of those variables from all the plots within a stand. Increasing shrub cover and slope were expected to decrease the density of *M. vimineum* within stands. Chapter 2 focuses exclusively on a plot-level analysis of the distribution data. At this scale, I hypothesized that increasing canopy and subcanopy cover would be strongly negatively related to invasion by lowering the amount of light reaching the forest floor. Further, richer and more water-retentive soils were expected to support denser populations of *M. vimineum*. Finally, the presence of potential dispersal corridors was expected to be tightly linked to the presence of invasion, and especially so with plots closer to the forest edge and potential seed sources.

Taken together, chapters 1 and 2 compare the influences on *M. vimineum* invasion at two different scales, that of the entire stand and of plant patches within stands. Since the factors controlling introduction to a site (stand-scale) may be different than those

influencing success once there (patch-scale), this multiscale approach is necessary to tease them apart.

In chapter 3, I focus on the role of seed dispersal in sustaining and expanding *M. vimineum* populations. Road- and waterways have been most often identified as the primary dispersal corridors of the species, and I surveyed populations along both of those dispersal corridors, as well as through nearby control habitat that had neither of those features. Transects were surveyed in both young and old stands to ascertain if dispersal patterns were different depending on the age of the forest. I expected that roads (trails) and streams would have higher presence and intensity of invasion than the control transects, whether they ran through young or old forests. However, I expected old forests to be less thoroughly invaded than young forests along the same transect types. I also monitored isolated (not on corridors) patches to determine rates of annual patch expansion, anticipating that most expansion would be very slow, except on steeper slopes. I expected the majority of the seeds, and seeds traveling the furthest, to be found downhill of the parent patches.

Finally, chapter 4 explores the demographic transitions of *M. vimineum* and their controls, by a seeding experiment under differing levels of shade and leaf litter depth. In a series of plots under a mature canopy, seeds were added with either the presence or absence of native shrub layers overhead, with litter depths manipulated as well. I hypothesized that seeds under shrub shade and deeper litter layers would experience higher mortality at all stages of life than those seeds with more light and less litter. In

addition, seeds sown on top of undisturbed litter were expected to perform more poorly than seeds sown in contact with the soil, due to radicle inhibition after germination.

In short, this study examines the invasion of one species at a variety of spatial scales, from the landscape down to individual plants, in order to better understand the constraints on the species at those differing scales. In doing so, it also expands our understanding of land use legacies and temporally-variable community invasibility. I found that community age and historical conditions were the most influential forces on the invasion pattern, and constrained the role of other population controls, suggesting that far more attention should be paid to these descriptors in consideration of management efforts.

CHAPTER 1

Historical and contemporary landscape constraints on the distribution patterns of an exotic annual grass in the eastern United States.

Abstract: A growing body of research is highlighting the important effects of age and land use history on the composition of plant communities, and for patterns of invasion into those communities. In order to better understand the role of these and other landscape factors in a plant invasion, surveys for the presence and abundance of the invasive annual grass *Microstegium vimineum* were conducted in central New Jersey in a variety of forest stands, with a range of ages and prior uses. A total of 1248 circular plots (5m radius) were surveyed in twenty stands, with the percent cover of *M. vimineum* estimated in each plot. For all stands, forest age explained the most variability among stands, with average slope and historical landscape connectivity also contributing explanatory power. When the stands were divided into old (> 80 years) and young (≤ 80 yrs.) categories, 94% of the variability among young stands was explained by five landscape variables (average shrub cover and slope, area, age, and current connectivity) while only 16% of the variability among old stands was explained by slope and area. All of these variables were negatively related to *M. vimineum* cover, except for stand area, which unexpectedly had a weak positive relationship to invasion. Knowledge of a small set of landscape variables can greatly enhance prediction and management efforts for younger forests, but smaller-scale processes are responsible for the large majority of variability in invasion among older forests.

Introduction

The majority of research on the processes of plant invasions has focused on traits conferring invasive tendencies to certain species or invasibility to particular habitats and communities (Stohlgren, Binkley et al. 1999; Alpert, Bone et al. 2000; Davis, Grime et al. 2000; Kolar and Lodge 2001; Cleland, Smith et al. 2004; Richardson 2004; Davis, Thompson et al. 2005; Lockwood, Cassey et al. 2005). Less frequently has work addressed the processes constraining invasion patterns across the network of habitats within a landscape context (Stohlgren, Chong et al. 2002; Pauchard and Alaback 2004; Deckers, Verheyen et al. 2005). Yet there has been an increasing interest in this level of interaction within plant ecology more generally, and it has resulted in very fruitful applications in such subfields as metapopulations (Wiens, Stenseth et al. 1993; Lindborg and Eriksson 2004; Kolb and Diekmann 2005) and optimal reserve design (Herzog, Lausch et al. 2001; Eberhardt, Foster et al. 2003; Kolb and Diekmann 2004). In general, this approach has illustrated the value of considering how higher-level factors (in either space or time) can influence the interplay of other factors influencing species success on the local scale (Dupouey, Dambrine et al. 2002; Foster, Swanson et al. 2003; Cleland, Smith et al. 2004). Especially in the area of invasion biology, which informs management decisions at multiple spatial scales, there is an increasing need to integrate landscape-scale studies into our understanding (Levine 2000; Honnay, Bossuyt et al. 2002).

Landscape factors influence local interactions primarily by constraining them spatially or temporally, thus allowing for local factors to interact in new ways, especially when the effects of those factors change along independent gradients (Rouget and

Richardson 2003; Gilbert and Lechowicz 2005). For a simple example, consider a habitat with the presence of optimal growing conditions for a particular species, which nonetheless may be unoccupied by that species if there is no dispersal vector also present to carry propagules into the site. Although many researchers have emphasized the importance of these ideas for rare and endangered plant species, they are just as relevant for weedy and invasive species (Hobbs and Huenneke 1992). For those invasive species capable of spreading through mature communities, their relative abundance in a particular habitat is likely to be limited by the position of that habitat in the larger landscape: its location relative to and connectivity with other mature habitats, its absolute size, and its ratio of edge to interior habitat (Brothers and Spingarn 1992). All of these descriptors are directly related to propagule infiltration into the habitat.

In addition to the contemporary spatial relationships of communities on the landscape, it is important to consider arrangements of the land in the recent past. Although several studies have shown persistent differences in the vegetation on adjacent farmed and non-farmed plots that can last up to 1800 years (Dambrine, Dupouey et al. 2007), it appears at least to be true that substantial differences from older communities are commonly present up to 100 years after land use cessation (Bellemare, Motzkin et al. 2002; Gerhardt and Foster 2002; Vellend 2004; Flinn and Vellend 2005). These differences have much to do with the relative proximity of propagule sources to recolonize abandoned landscapes (Brunet and Oheimb 1998; Bossuyt and Hermy 2001; Lockwood, Cassey et al. 2005), as well as such variable influences as herbivore pressure (Pedersen and Wallis 2004) and altered soil legacies (Lewis et al. 2002, Fraterrigo *et al.* 2005). In the case of invasive plants, the condition of the landscape during the time of a

species' establishment in a region is likely to be just as influential as contemporary conditions in determining the extent of that species' invasive range (Graae, Okland et al. 2004; Jongejans, Skarpaas et al. 2007). Especially for those species that can physically modify the habitat for species that might follow (e.g.- woody plants in early successional systems)(Kourtev, Ehrenfeld et al. 1998; Ehrenfeld, Kourtev et al. 2001; Lichstein, Grau et al. 2004), the presence of historical establishment opportunities may allow for dominance in locations where the species may struggle to become established under current conditions.

One invasive species gaining prominence along the Atlantic seaboard of the U.S. over the last 40-50 years is *Microstegium vimineum* [Trin.] A. Camus (hereafter *M. vimineum* or stiltgrass), which was first recorded in the country in Knoxville, TN (1919) (Fairbrothers and Gray 1972). It is an annual, C₄ grass that does extremely well in riparian areas, roadsides, field margins and other habitats with frequent disturbance (Barden 1987; Redman 1995). The species has also demonstrated the ability to invade the herbaceous layer of minimally-disturbed forests, however, and as such is a growing concern for the threat it poses to native herb diversity (Belote and Weltzin 2006; Judge 2006). As an annual plant dependent on seed production rather than clonal growth for population expansion (Gibson, Spyreas et al. 2002), *M. vimineum* is an ideal plant for studying the relationship of invasion to past and present landscape arrangement. The species was being widely introduced to the landscape at the same time as many formerly agricultural fields were slowly returning to forest cover (mid-20th century) (Foster 1992; Luce 2001). Because the species is ultimately limited by deep shade, it is likely that much of the scrub forest cover was more conducive to its establishment than mature forest

would be (Cole and Weltzin 2004; Leicht, Silander et al. 2005). In the intervening decades, and even as forests in the region have developed fuller canopies, the species may maintain populations in many forests because of its historical presence there (Hunt and Zaremba 1992). Since forest age is also often correlated with such variables as topography and surficial geology, these factors too tend to show strong relationships to the presence of *M. vimineum*.

The purpose of this study was to examine the relationship of *M. vimineum* distribution and abundance to contemporary landscape variables, namely forest area, shape and connectivity, and historic landscape variables, specifically forest age and prior land use, as well as former area and connectivity. It was hypothesized that smaller, younger, and more isolated forests would have greater abundances of the species than would larger, older, and less isolated forests, due primarily to more intense propagule pressure over a longer time period and more favorable edaphic conditions in such forests. In addition, I expected to find higher abundances in forests with level slopes and deeper, richer soils, in large part because of their favorable growing conditions. Such soils are also highly confounded with forest age, since they were both more suitable for earlier agriculture (lower slope positions and deeper soils) and more likely to retain a legacy of enriched soils post-abandonment.

Materials and Methods

This study took place in the Sourland Mountain region of west-central New Jersey, USA (approximate coordinates: 40°23'N 74°50'W). The Sourlands are a 28-km long ridge (40-150m in elevation), composed of Triassic-era igneous diabase intruded

into the dominantly sedimentary rock terrane of the surrounding Piedmont. The diabase rock weathers slowly, leaving extremely stony soils with abundant large boulders in some landscape positions. At the turn of the 20th century, like much of the eastern U.S., level land in the region was predominantly cropland, whereas steeper and rockier areas were retained as forest lands. A topographic survey performed by the NJ State Geologist in the late 1880s (Cook and Vermeule 1889) mapped in detail the locations of forested tracts of land and farm field boundaries. In the first half of the twentieth century, as the economics of small-scale farming changed, much of the region's population left, creating a mosaic of old secondary forests and young forests growing over old fields and pastures of various ages. This trend accelerated after World War II, leaving a predominantly forested landscape by the 1960s (Luce 2001; Banisch Associates 2004). Recent changes in the region have included encroaching suburban development and traprock (diabase) quarrying.

Information on current and historical locations of forests in the area was obtained from aerial photographs archived by the NJ Department of Environmental Protection (Trenton, NJ) and processed using ArcMap. Orthophotographs from 2002 (1' resolution) were used for contemporary conditions as they represented the most recent photography available at the time of the study. The earliest photos of the region are from the mid 1930s, and have been hand-mosaicked to produce a composite image (6.5' resolution). These two sets were then viewed in comparison under the same projection to locate stands present before and after circa 1935. Photos from the intervening decades (taken every 7-10 years) were manually examined to more accurately establish the age and prior land use of forests that regenerated after the 1930s. Specific study sites were selected to

span the length of the region, and in all cases paired a young stand (≤ 70 yrs. old; pasture/old field or crop field in 1930) with an adjacent old stand (≥ 80 yrs. old; closed canopy by 1930, also present as far back as the Cook/Vermeule study in 1890) (Fig. 1).

Within each stand selected for the study, circular plots (5m radius) were surveyed along radial transects from the stand center, running out in eight directions along the N-S, NE-SW, E-W and SE-NW axes (Fig. 2). For the five largest stands, plots were spaced every 50m along the transects, but the majority of plots were spaced 25m apart. This resulted in each stand containing at least 40 plots, with a maximum of 105 in the largest stand. In the summer of 2006, each plot was visited and the percent cover of *M. vimineum* present was visually estimated into cover classes with the following medians: 0, 0.05 (one to several plants), 0.5, 3, 7.5, 12.5, 17.5, 22.5, 30, 42.5, 60 and 85%. This breakdown was designed to more effectively capture the fine gradations between plots at low levels of invasion intensity. In addition to stiltgrass cover, the percentage of cover due to shrub species was estimated, and the three dominant tree species providing canopy over the plot were noted in descending order. The percentage of canopy closure was determined using a spherical densiometer, and averaging four readings taken from each plot (each 1.5m from plot center on cardinal directions). I also noted the presence of several potential seed dispersal corridors running in or near each plot, as well as areas likely to represent favorable habitat or points of introduction for the species. Corridors noted included streams, apparent areas of surface water drainage (i.e.-leaf packs or scoured surface), foot trails (human or deer), motorized paths (i.e.- two-tracks), and traces of old trails/roads. Favorable habitat sites and possible introduction points noted were vernal pools and remnants of human land use (stone fences, building foundations,

etc.). The exact position of each plot was captured by a GPS unit in the field or by interpolation from nearby points if dense canopies at a particular point made satellite detection marginal. Using these locations and the series of historical aerial photographs as described above, a more exact age for each plot (40-100+ years, depending on when forest regeneration was first seen in the photographs) was estimated. These plot ages were then averaged within each stand to more accurately separate the young stands by age.

Stand characteristics such as area, perimeter, and connectivity were determined using ArcMap on both the 1930s and 2002 photos. Connectivity was measured as the percentage of each parcel's perimeter that was continuous with forest in both time periods. Higher percentages of connectivity to adjacent forest represent greater embeddedness in the overall forest matrix and presumably greater distance from anthropogenically-dominated land covers that would have been the initial points of introduction for the species into the landscape. The percentages of each parcel's perimeter that were continuous with forest in the 1930s (Forest-30s) and in 2002 (Forest-00s) were both calculated. Data on the slope, aspect, and hillshade of each plot were calculated from 10m-resolution digital elevation models created by the NJ DEP (NJ GIS, Trenton, NJ). Soil series data were derived from the SSURGO databases developed by the USDA-NRCS. Overall, 690 plots in ten old forest stands and 558 plots in ten young stands were sampled.

In order to see if significant patterns of spatial autocorrelation in *M. vimineum* cover emerged within each stand, a Moran's I value was calculated for the plots within

each. Semivariograms were then generated using ArcInfo and the range of autocorrelation was estimated for the stands. Spatial autocorrelation was more often present and was clearer in old stands than young. Z-scores for young stands ranged from -0.136 to 4.955, with a mean of 2.213, while those for old stands ranged from -0.453 to 6.795 (mean = 2.754). In general, even stands with highly significant Moran's I values (here, clustered) had range values between 35 and 85m, meaning that autocorrelation extended no more than 2-3 plots. Non-significantly correlated stands had ranges of 12-30m, and thus were not correlated past a plot's immediate neighbor.

Data on *M. vimineum* presence in relation to these variables was analyzed at both stand and plot scales using SAS v9.1. Variables summarized by stands were analyzed with PROC TTEST when being grouped by age (old and young). Pearson correlations between independent variables were checked in order to simplify the list of variables and avoid redundancies in modeling (PROC CORR). PROC REG was used to construct a multiple regression model of stand-level variables, with variance inflation factors (VIFs) tested to assure multicollinearity was not overly influential on the model. Variables with VIFs higher than 1.3 were excluded from further analysis. Some of the variables are properties of the stand itself (i.e.- area, forest connectivity) while others are the mean of all plot values within each stand (i.e.- slope, shrub cover, age [yrs.]). In all cases, mean *M. vimineum* cover of the plots within the stand was the dependent variable. Simple linear regressions were also run to further examine the effect of individual variables (stand area, forest connectivity [1930s and 2000s], age, total shrub cover, and slope). Linear models (PROC GLM) were used to examine several categorical variables at the

plot-level (aspect and soil category). Multiple contrast tests always used Tukey's honestly-significant-difference (HSD).

Results

Stand Descriptions

The overall mean percent cover of *M. vimineum* was 14.3% ($\pm 0.7\%$), but there was a sharp division between average cover in old and young stands (Table 1). For most other landscape-level descriptors the young and old stands were comparable. Interestingly, in the mid-1930s most of the stands or fields had a similar amount of forest around them, reflective of the general heterogeneity of this forested landscape during periods of active agriculture. All stands but one also saw an increase in their continuity with forest between the 1930s and 2002, and the significant difference between ages by 2002 is due entirely to the clustering of the old stands around very high values of adjacent forest cover. This partly reflects the selection method for old stands in this study, as they were initially chosen from the core of existing forests to minimize the confounding influence of edge effects. Thus they have very high connectivity to other forests.

Stand-Level Regression Models

Simple linear regression of mean *M. vimineum* cover by stand against a number of independent variables clearly shows that the stand level of analysis does a poor job of explaining variability in invasion for old stands, but a fair job for young ones (Table 2). A multiple regression model of all twenty stands revealed that age had by far the most significant contribution to explaining mean *M. vimineum* cover (Table 3). Although each

stand was classified as either young or old, better age estimates for the young stands were determined by averaging the age (in decades) for all plots within each stand. This is due to small areas of tree cover (i.e.-hedgerows, rock piles) existing in the midst of former fields that established before the rest of the field was finally abandoned. Much of the significance of this relationship is due to the low average invasion of the old stands, but even within the younger stands increasing age results in a lower percentage of invasion (Fig. 3). Historic forest connectivity and average slope also have a negative relationship with stiltgrass invasion. Unexpectedly, stand area was positively related to invasion. Although the individual regression was significant, it did not contribute much to the overall explanatory power of the model, which accounted for 76.5% of the variability among stands.

A second set of multiple regression models was created to tease apart important factors in both old and young stands (Table 4). The resulting model for old stands included area and slope, but explained very little of the variability (16%). In contrast, the model for young stands explained the vast majority of the variability (94%) and included total shrub cover, contemporary forest continuity and age as important factors, as well as area and slope. A closer look at area reveals that the effect is due almost entirely to one data point, the largest young forest stand (Fig. 4). This stand has very little shrub cover under a red maple canopy, and thus has extensive swards of *M. vimineum* in the herbaceous layer. When this stand is removed from the analysis, stand area is no longer a significant factor in the regression. The effect of slope, however, is also noticeable within young stands, although it alone does not have a significant regression for old stands (Fig. 5). Although stands with gentle slopes overall have a high degree of variability in terms

of invasion cover, stands on steeper slopes have much less *M. vimineum* present, especially in the young forests.

The single most important variable for young stands was total shrub cover in the plots, which was inversely related to mean *M. vimineum* cover. Shrub cover was not significantly related to invasion in old stands, which causes the overall regression of this variable for all stands to be nonsignificant. Within young stands, though, increasing shrub cover, whether of exotic or native species, has a strong limiting effect on stiltgrass invasion (Fig. 6). This effect is probably due to shrubs outcompeting the herb for light, and since many young stands are poor in terms of shrub cover, those which do have shrubs are strongly differentiated from those that do not. Stand age (as a function of plot means) and contemporary forest connectivity (Fig. 7) are the other contributing variables for young stands.

Plot-Level Variables

Topography and soils also tend to have effects on the abundance of *M. vimineum* at different plots within stands. Slope percentage was strongly negatively related (-0.6456 % *M. vimineum* / 1% slope; $p < 0.0001$) to the abundance of *M. vimineum* across stands, although there was a high degree of variability among plots ($r^2 = 0.0496$). Separated into slope categories, it is clear that much of the significance of slope is due to high levels of *M. vimineum* on the most level sites (Fig.8b), as densities of stiltgrass were statistically

indistinguishable at plots with a slope $> 5\%$. In other words, there is a threshold effect between 5 and 10% slopes, above which stiltgrass cover drops quickly, but below which a wide range of stiltgrass densities can be found. Slope aspect of the plots was also significant in predicting the abundance of stiltgrass (Fig. 8a), with south-facing slopes having the highest levels of the species, followed by west and east slopes, and finally north-facing slopes. Including the interaction between slope and aspect in a multivariate model yields a significant result ($F_{26, 1245} = 6.28, p < 0.0001$), although it is due more to the slope ($F_6 = 10.03$) and the slope*aspect interaction ($F_{17} = 2.01$) than to aspect ($F_3 = 1.86$ [ns]).

The soil type underlying each plot was also associated with *M. vimineum* cover, in large part because they are correlated with local topography and slope position. In particular, well-drained soils derived from igneous rock (diabase) had dramatically lower cover than soil weathered from other sources (Fig. 9). Moist igneous soils had intermediate amounts of *M. vimineum*, and plots on sedimentary soils had significantly higher levels of invasion. There was no statistical difference between moderately well-drained and poorly-drained sedimentary soils, however, in part because most of the poorly-drained plots are actually in perched water table situations on the crest of the Sourland ridge. Thus, they have not been as historically exposed to *M. vimineum* propagules as the bulk of the moderately well-drained soils, which tend to be on the lower flanks of the slope. A model to compare these categories in terms of invasion is highly significant ($F_{4,1244} = 35.47, p < 0.0001$). A two-way ANOVA with soil types and age is also very significant ($F = 61.24$) with both variables and their interaction contributing. The interaction effect is due to very high invasion levels on young,

moderately-drained sedimentary soils. In contrast, poorly-drained sedimentary soils are the most invaded in old forests.

Discussion

Success of *M. vimineum* invasion on the landscape scale was strongly associated with a number of variables, but the importance of forest age dwarfs any of the others. Age alone accounts for nearly 60% of the variability in invasion among forest stands. This significance is likely due to a number of conflated variables, chief among them biotic resistance due to denser levels of shade from shrub and tree strata in older forests (Cole and Weltzin 2004; Flory, Rudgers et al. 2007), as well as the steeper slopes that made these forests less accessible for human use in the first place. Although other variables, including shrub cover, slope and forest connectivity are important predictors, knowledge of a stand's age is extremely useful for understanding and attempting management of *M. vimineum* invasion across an entire landscape.

Although *M. vimineum* has only been known in the study region for about 60 years (Snyder 2004), most forests within the range of 40-75 years of age appear to offer favorable habitat for *M. vimineum* in the early stages of its spread. Young forests already possessing a robust shrub layer or those on steeper slopes do have lower levels of invasion than their counterparts, however. Much of the shrub cover in these young forests was composed of exotic shrubs (*Rosa multiflora*, *Berberis thunbergii*, etc.) though, so they are still heavily invaded in most cases. In either case, the forest development of the

landscape in the 1930s or '40s is clearly of importance in determining the relative susceptibility of different stands to stiltgrass or exotic shrub invasion. As is the pattern in much of the eastern U.S., the Sourlands have experienced a large increase in forest area over the last 75 years, from 22% of the landscape in forest in the mid-1930s to 56% in 2002 (Fig. 10). This period is coincidental with the introduction or rapid expansion of many exotic forest species. As DeGasperi and Motzkin (2007) documented for *B. thunbergii*, prior windows of good establishment conditions may have allowed many exotics to become prevalent members of communities that would experience less invasion under current conditions. In the case of *M. vimineum*, it is more likely that younger forests contain a suite of conditions that are more favorable for its establishment, since the development of vertical forest strata over time is eventually effective at excluding the species.

Another important ecological change over the last few decades has been the rapid increase in white-tailed deer densities, which further retard development of robust shrub layers through their browsing (Pedersen and Wallis 2004; Rooney, Wiegmann et al. 2004). These herbivores may be indirectly altering competitive dynamics between understory species, thus allowing unbrowsed *M. vimineum* to expand its distribution at the expense of heavily-browsed native shrubs (Griggs, Rock et al. 2006). Since deer densities are even higher in younger stands (often those closest to the edge of the forest matrix), their presence exacerbates the high levels of invasion within such forests (Adams 2003). Older stands, in part because of their steeper slopes and less accessibility, have tree canopies that intercept more sunlight, sustain extensive shrub layers where light

permits, and are farthest from the initial seed sources of stiltgrass. In concert these factors help to explain the low incidence of *M. vimineum* invasion in older stands.

Lower propagule pressure and more diverse native plant communities likely also explain why stands that are part of larger forest complexes tend to be less invaded than stands which are more isolated in a matrix of non-forest habitat. This trend was even true when considering historic connectivity, although it was not a large effect relative to slope and age. Numerous recent studies have shown the importance of surrounding forest habitat for the reestablishment of native forest plants after agricultural abandonment (Kolb and Diekmann 2004; Flinn and Vellend 2005; Flinn and Marks 2007; Hermy and Verheyen 2007). Thus, it can take longer for potential native competitors to reach a regenerating forest if it is isolated than recolonization would in a more highly-embedded young stand. The importance of connectivity may have been clearer in a landscape that was not as highly fragmented overall as in this study.

Interestingly, larger forests were more invaded than smaller ones, and significantly so for young stands. This is somewhat surprising since larger stands have a greater proportion of their area in core habitat, which in many situations experiences less invasion pressure and less deer herbivory than edge habitat (Adams 2003; Cadenasso and Pickett 2001). If the outlying young site is removed, however, the overall trend is towards decreasing invasion with an increase in stand area (Fig. 4). It could be that I did not find a strong relationship between area and invasion in this study due to the relatively small area of the stands (most were under 40 ha), and generally high fragmentation of these forests in a highly human-dominated system.

Patterns of topography and soil series also have a prominent structuring influence on *M. vimineum* invasion. The species has clearly been most successful at invading level or gently sloping sites, preferably on a southern aspect. In contrast, it is only rarely found on steep slopes with northern and, to a lesser extent, eastern exposures. As with many plant species, aspect is likely important because it largely determines the amount of sunlight that plants receive during the growing season, as well as the amount of water lost through evapotranspiration. Since *M. vimineum* uses the C₄ photosynthetic pathway, it is not surprising that it does better relative to many native herbs in the slightly warmer and drier forests on the south-facing slopes of the region (Winter, Schmidtt et al. 1982; Claridge and Franklin 2002). Slope steepness is likely influencing invasion through several mechanisms. First and foremost, local hydrology on level areas tends to include greater pooling and flooding extent at times of high water, whereas steeper slopes tend to concentrate flow into narrow stream channels. Since the species is often hydrochorous (Scholz and Byfield 2000; Gibson, Spyreas et al. 2002), the former situation encourages establishment of dense stands, even as the latter still allows for focused dispersal across the landscape (Peskin 2005). Particularly in the Sourlands, where level ridgetop soils often have a clay fragipan 20-30cm below the surface, vernal pools can be an effective route for widespread seed dispersal and patch establishment. Second, level areas tend to be those that were more amenable to cultivation or pasturing when the region was more agricultural, and so often contain the youngest forests, which can be heavily invaded by stiltgrass. Finally, level areas are often closer to the edge of my studied stands, and thus are more susceptible to invasion pressure, especially those created by white-tailed deer herbivory.

In summary, knowledge of a forest's age and slope position can greatly enhance prediction of *M. vimineum* invasion on the landscape scale. Combined with patch-level observations on shrub communities and soil series, these variables explain over 75% of the variability in invasion among stands, and can be a powerful tool as land managers assess alternate management strategies for this species.

Table 1. Descriptions of key landscape characterizations of the *a priori* young (<75 yrs old) and old (>80 yrs old) forest stands used in this study. Parentheses indicate one standard error, and significant differences between young and old using a two-tailed, two-sample t-test are indicated by asterisks.

	Young Stands (n =10)				Old Stands (n =10)			
	Mean (s.e.)	Median	Min.	Max.	Mean (s.e.)	Median	Min.	Max.
# of Plots *	55.8 (3.3)	54.5	40	73	69.0 (4.64)	68.5	46	105
Area (ha)	24.99 (5.67)	19.07	8.43	70.83	39.60 (8.57)	27.68	17.16	102.7
Perimeter (km)	2.712 (.348)	2.213	1.331	4.726	2.970 (.197)	2.960	1.761	4.031
P:A (m/ha)	127.8 (15.7)	119.9	66.7	252.8	93.9 (11.3)	98.6	52.0	152.5
Age (years)**	64.9 (3.4)	62.7	52.7	88.6	100 (0.0)	100	100	100
Slope (%)	5.9 (1.6)	3.5	1.3	16.9	9.1 (1.7)	6.5	3.9	16.1
Total Shrub Cover (%)	33.1 (5.5)	29.6	13.7	66.6	19.0 (4.6)	14.5	4	45
% Continuous w/ Forest ('30s)	61.0 (9.3)	68.9	0	97.6	60.5 (6.2)	57.3	30.2	84.7
% Continuous w/ Forest ('02) *	77.4 (7.7)	86.0	17.4	96.7	96.0 (1.5)	97.3	85.0	100.0
<i>M. vimineum</i> % Cover (by stand) **	24.7 (4.6)	23.8	7.0	51.2	6.2 (1.4)	5.6	1.4	14.1

Significant differences between the means of old and young stands for these categories were checked using two-sample t-tests. * $p < 0.05$ ** $p < 0.01$

Table 2. Simple linear regressions of all variables used at the stand level in modeling *M. vimineum* abundance. Significance was calculated using *F*-statistics. Variables that are significant in multiple regression models are boldfaced.

Dependent	Independent	Overall Sig.	b	r^2	Old Sig.	b	r^2	Young Sig.	b	r^2
Mean <i>M.v.</i> Cover	Mean Plot Age	***	-0.551	0.584	n/a	n/a	n/a	ns	-0.686	0.267
	Mean Plot Slope	*	-1.28	0.234	ns	-0.09	0.012	ns	-1.559	0.305
	Mean Plot Hillshade	ns	-0.116	0.008	ns	-0.134	0.132	ns	-0.432	0.089
	Mean Plot Shrubs (Native)	ns	-0.203	0.017	ns	0.101	0.023	ns	-0.553	0.181
	Mean Plot Shrubs (Total)	ns	-0.061	0.006	ns	0.021	0.005	*	-0.623	0.562
	Mean Plot Shrubs (Exotic)	ns	-0.014	0.000	ns	0.004	0.000	*	-0.850	0.487
	Stand Area	ns	0.037	0.004	ns	0.052	0.105	ns	0.486	0.363
	Stand Perimeter	ns	0.003	0.025	ns	0.001	0.040	ns	0.005	0.155
	Forest-1930s	ns	-0.135	0.055	ns	0.004	0.000	ns	-0.203	0.171
	Forest-2000s	*	-0.335	0.217	ns	-0.100	0.013	ns	-0.129	0.047

Table 3. Forward selection multiple linear regression model for the mean *M. vimineum* cover in all twenty surveyed stands. ‘Area’ and ‘Forest-30s’ are a property of an entire stand, while ‘Age’ and ‘Slope’ are the mean values of those variables from every plot within a stand. AIC for this model was 85.72, a model with age alone has AIC of 91.18.

	β	S.E.	t	p	r^2
Age	-0.539	0.103	-5.25	0.0001	0.584
Slope	-0.638	0.374	-1.71	0.1086	0.234
Forest 1930s	-0.13	0.074	-1.76	0.0987	0.055
Area	0.232	0.08	2.88	0.0114	0.004
Total			$F_{4,19} =$ 12.22	0.0001	0.765

Table 4. Multiple linear regression models for mean *M. vimineum* cover in ten old and ten young stands. As above, ‘Area’ and ‘Forest-00s’ are a single value for each stand, while ‘Slope,’ ‘Total Shrubs’ and ‘Age’ are mean values from all of the plots within each stand. $AIC_{Old} = 32.36$, $AIC_{Young} = 36.51$

Old	β	S.E.	t	p	r^2
Area	0.065	0.058	1.11	0.3033	0.105
Slope	-0.203	0.300	-0.68	0.5208	0.012
Total			$F_{2,9} = 0.67$	0.5429	0.160
Young	β	S.E.	t	p	r^2
Total Shrubs	-.377	0.124	-3.03	0.0386	0.562
Area	0.421	0.124	3.39	0.0276	0.363
Slope	-1.114	0.471	-2.37	0.0772	0.305
Age	-0.066	0.258	-0.26	0.8106	0.267
Forest-00s	-0.109	0.108	-1.01	0.3698	0.047
Total			$F_{5,9} = 12.14$	0.0157	0.938

Figure 1. Land use map of the Sourland region, based on 2002 land cover surveys. Most of the ‘Wetlands’ indicated on the map are forested (e.g. vernal pools/swamps). ‘Urban’ and ‘Barren Lands’ are either suburban development or rock quarries. Also shown are the 20 forest parcels used in this study’s survey, with young parcels crosshatched and older ones with simple hatching. The inset map indicates the location of the Sourlands within New Jersey.

Figure 2. Sampling design example. Shown are two old and two young forest stands at the Somerset County Sourland Reserve. Each dot within the stands represents a surveyed plot. Aerial photography is from 2002.

Figure 3. Relationship of stand age to mean *M. vimineum* cover in twenty forest plots. The regression is highly significant ($t = -5.02$, $p < 0.0001$).

Figure 4. Effect of stand area on mean abundance of *M. vimineum*. The overall regression for these points is not significantly different from a line with slope = 0. The young stand outlined in red is an outlier in terms of area (see text).

Figure 5. Regressions of mean stand slope against *M. vimineum* cover for young and old stands. The overall regression has an adjusted $r^2 = 0.192$ and is significant ($t = -2.35$, $p = 0.0305$).

Figure 6. Relationship of total shrub cover to *M. vimineum* cover in young and old forests stands. The overall regression is nonsignificant.

Figure 7. Effect of contemporary connectivity of forest stands on abundance of *M. vimineum*. The overall regression of these stands is significant ($p = 0.0387$), and has a strong negative slope (-0.335% *M.vimineum* / 1% Continuity).

Figure 8. The relationship of plot aspect **(a)** and slope **(b)** to abundance of *M. vimineum*. Bars represent one standard error, and aspects with the same letter label within each graph are not significantly different from each other. Numbers in columns are the number of plots surveyed in each category.

Figure 9. Abundance of *M. vimineum* in relation to the underlying soil type for each plot. Bars represent one standard error, and categories with different letter labels are significantly different from each other at $\alpha = 0.05$ (Tukey’s HSD). Numbers in columns are the number of plots in that category. “Dry Ig” = well-drained igneous (Legore), “Moist Ig” = moderately well-drained igneous (Mount Lucas, Neshaminy), “Moist Sed” = moderately well-drained sedimentary (Lansdale, Reaville), and “Wet Sed” = poorly-drained sedimentary (Chalfont). Alluvial soils included Royce, Rowland and Watchung Silts.

Figure 10. Land cover maps of the Sourland region (NJ) in the mid-1930s (left) and in 2002 (right). Forest area in both is shown in dark gray, and agricultural lands are pale gray.

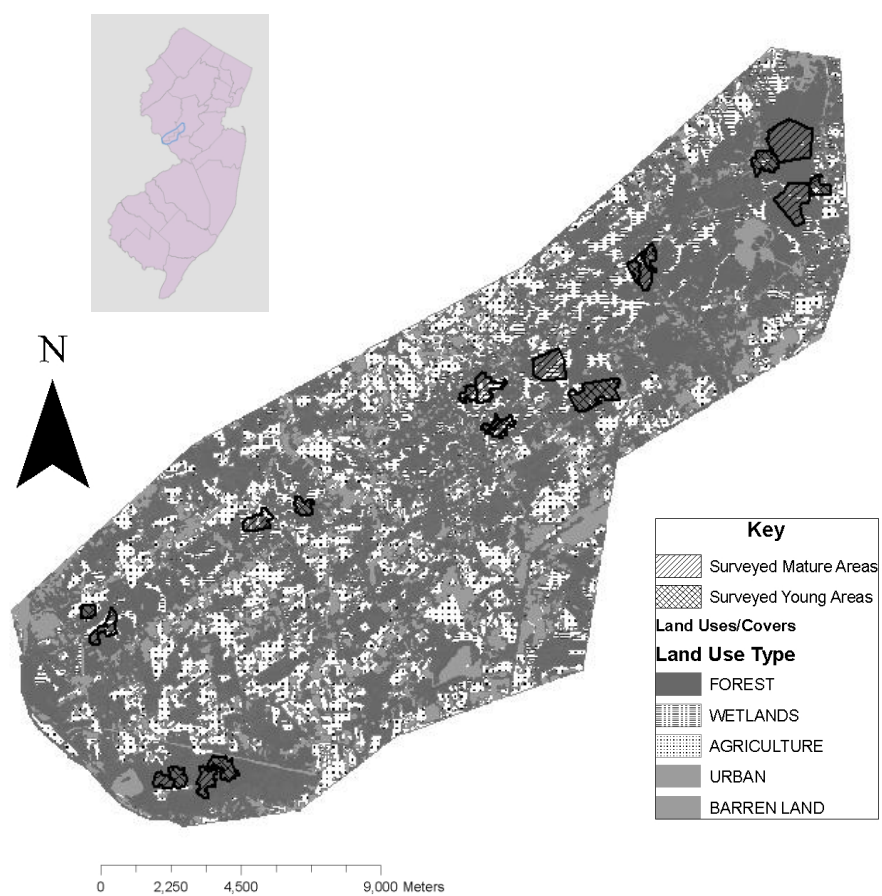


Figure 1

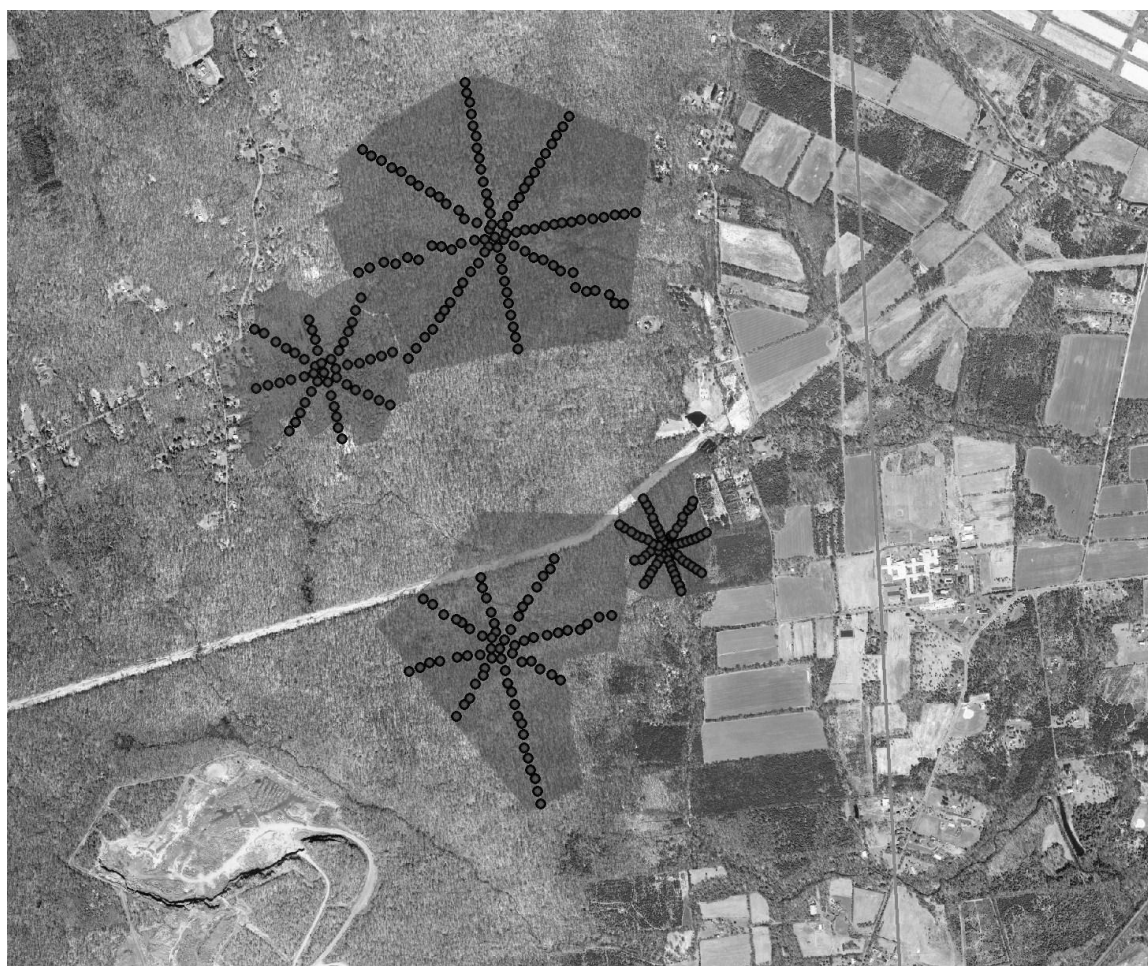


Figure 2

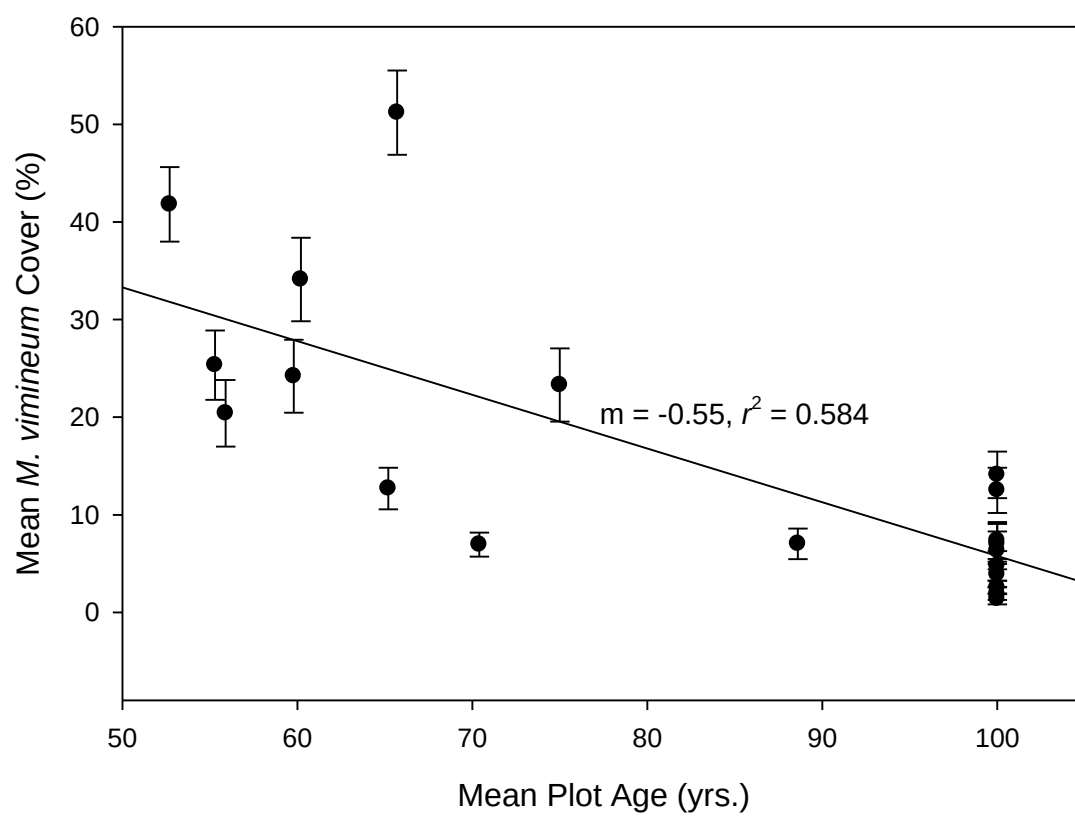


Figure 3

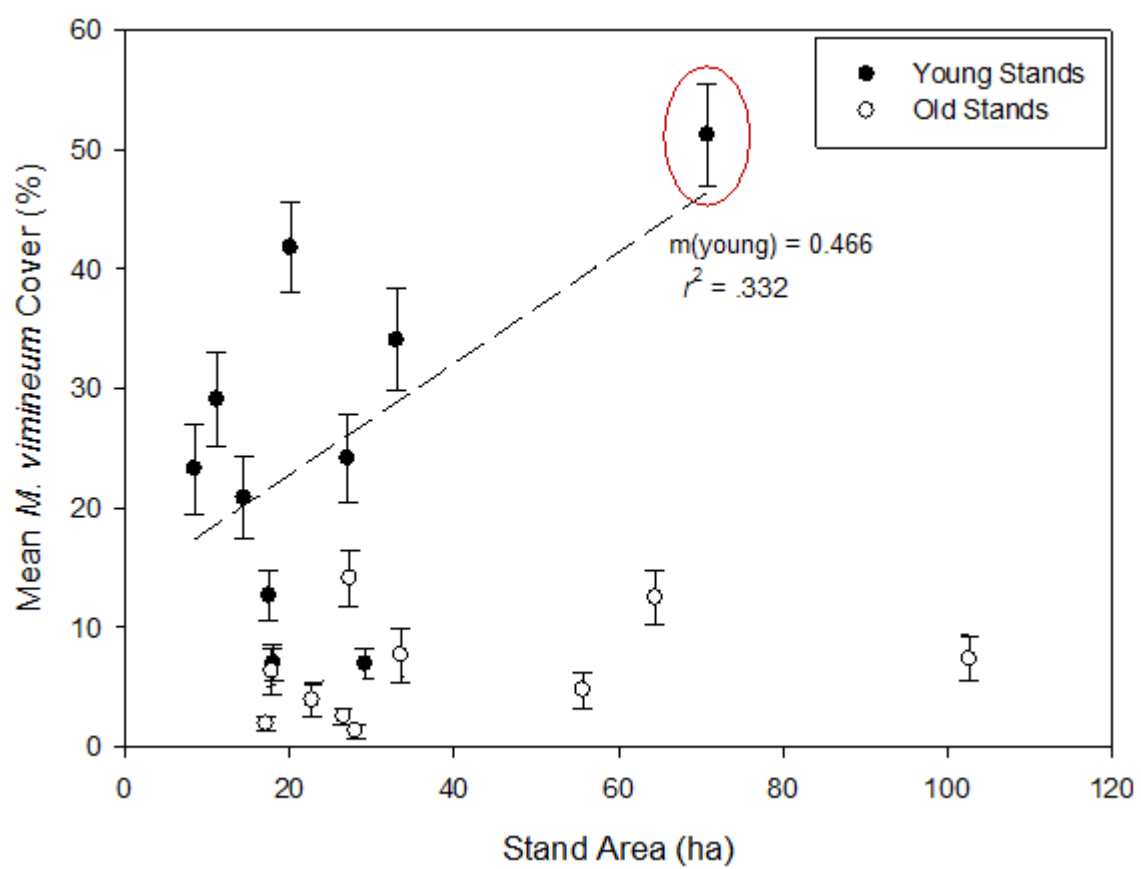


Figure 4

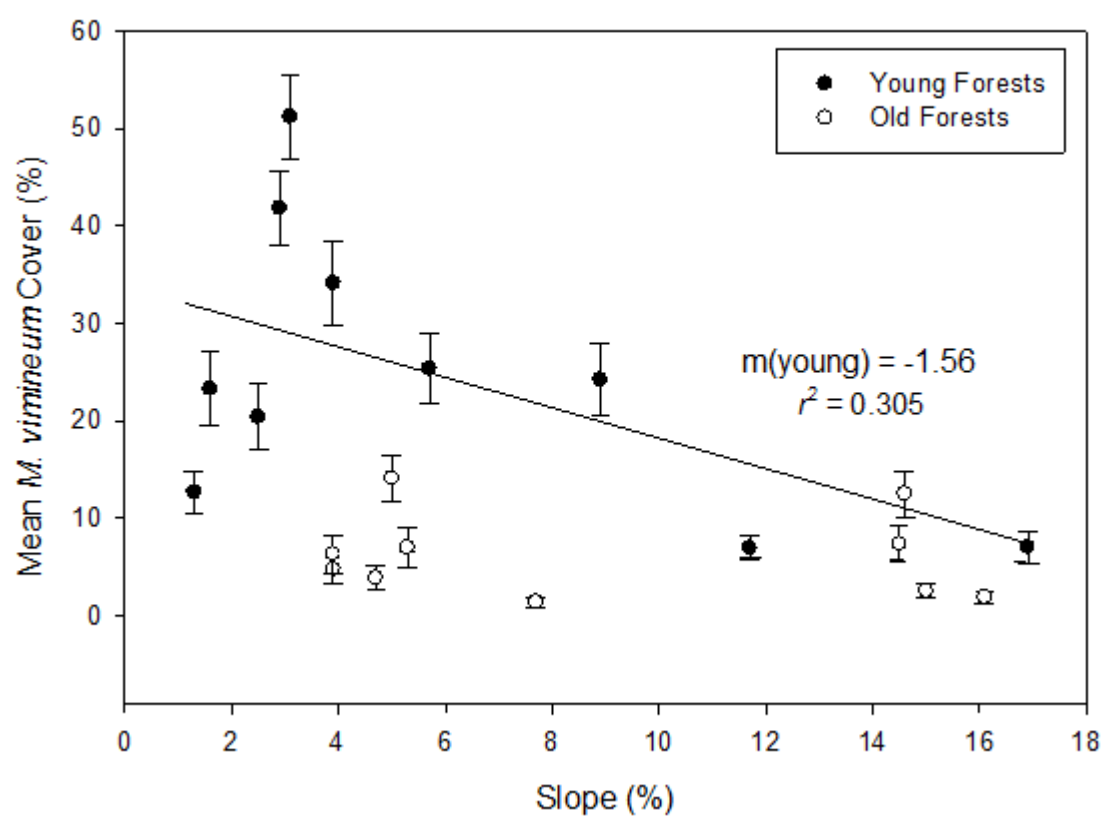


Figure 5

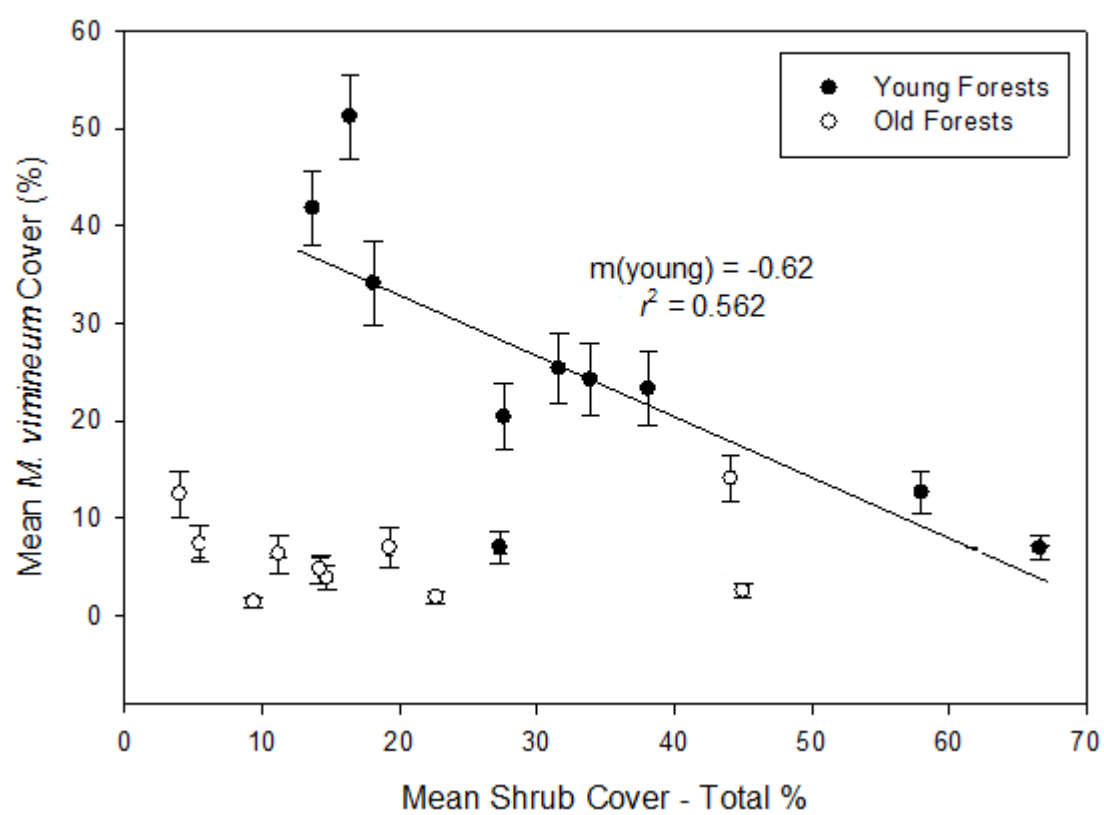
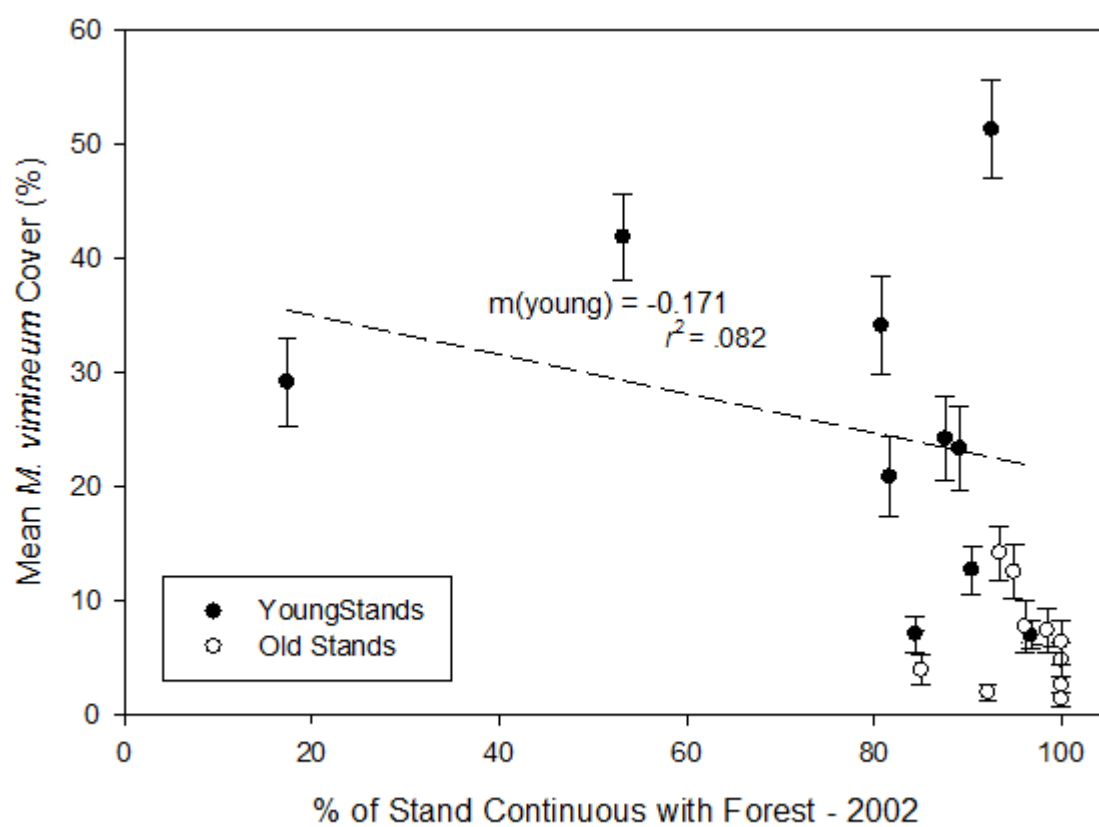
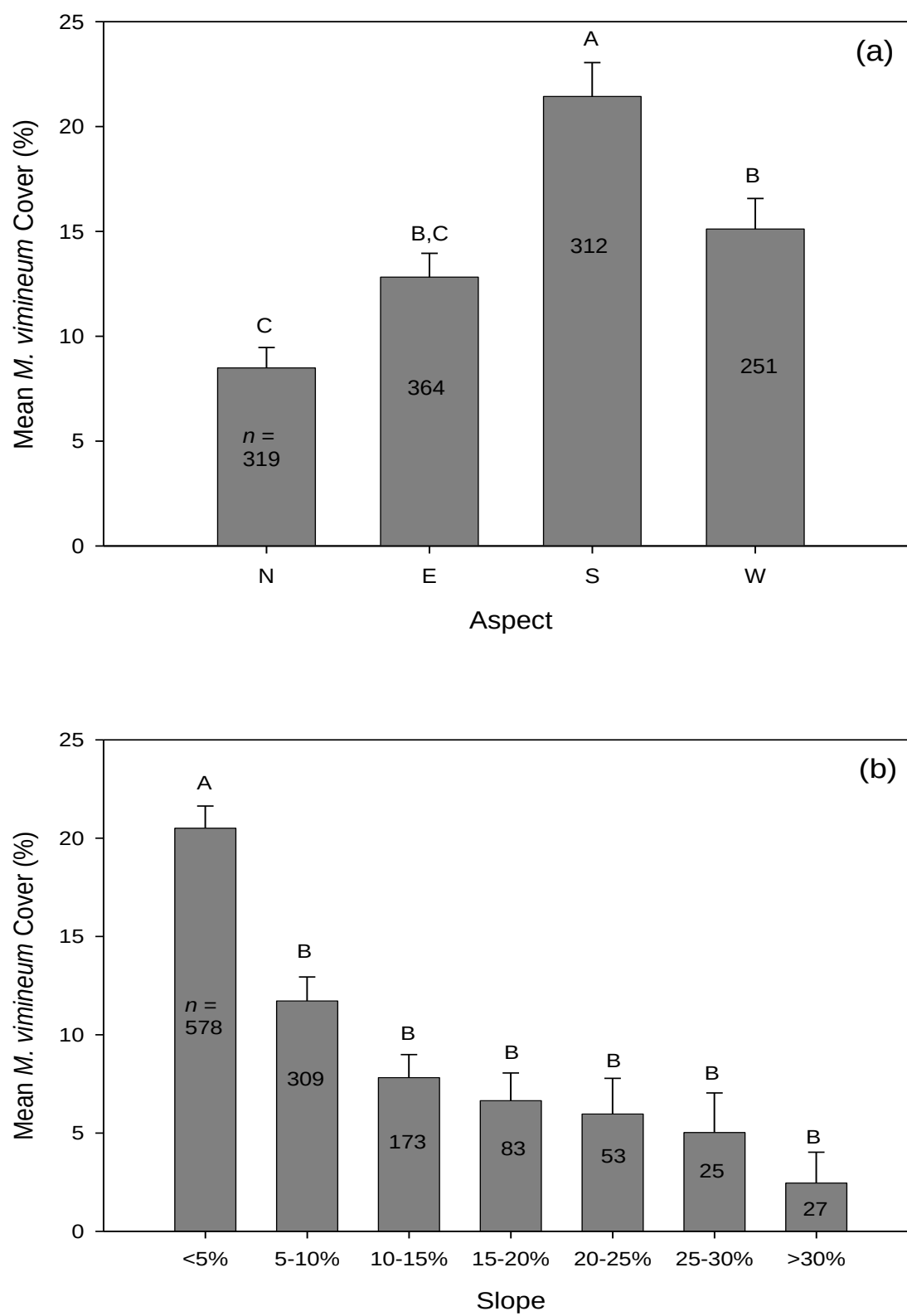


Figure 6

**Figure 7**

**Figure 8**

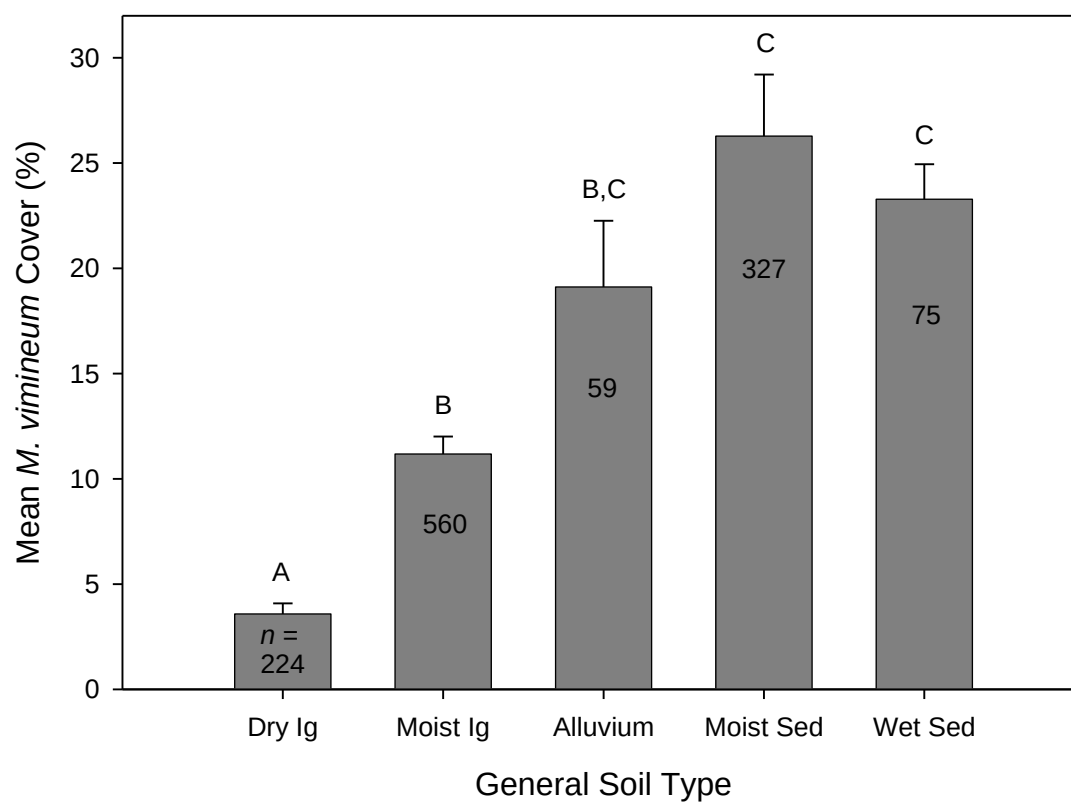
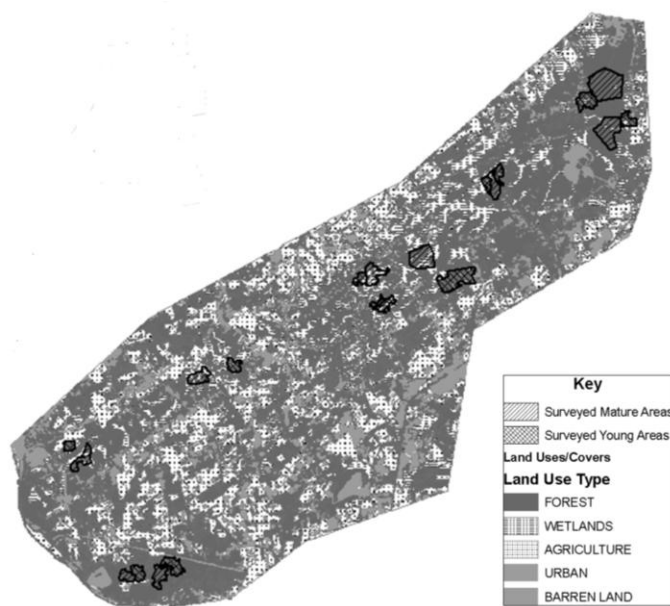


Figure 9



1930s



2002

Figure 10

CHAPTER 2

Forest age and land use history constrain the invasion patterns of an annual grass in eastern hardwood forests of the United States.

Abstract: Increasingly, researchers are recognizing that limiting factors on species distributions can be arranged hierarchically, and that historical legacies often contribute to these overarching constraints. The applicability of this approach to invasive species has not been very well considered, however, even though it could greatly strengthen habitat-specific management approaches. This study examined the distribution of the invasive grass *Microstegium vimineum* in a complex forested landscape in relation to a number of abiotic and biotic variables, using a combination of logistic regression and regression tree analyses. The species was found in a large majority of plots surveyed (77%), but occurred most frequently and most abundantly in younger forests. Invasion in younger forests was most constrained by underlying soil type, distance-to-edge and the presence of shrub canopies, while older forest invasion patterns were strongly determined by the location of canopy gaps and seed dispersal pathways. The results suggest that although underlying physiological constraints on the species' expansion are consistent across habitats, their relative importance varies in forests of different ages, and control efforts should be adjusted to reflect those differences.

Introduction

Although research has illuminated causation of invasion patterns for many species, overarching generalities remain elusive. In part this may be due to the wide diversity of invasive species and invaded habitats, which leads to a large number of permutations on common explanations. Another underemphasized reason for this difficulty may be the contingent nature of limiting influences on individual species: the relative importance of controlling factors can vary in response to one or more overarching environmental factors (Belyea and Lancaster 1999; Didham, Watts et al. 2005). This is true for both native and non-native species (Davis, Thompson et al. 2005), and could account for the importance of a particular factor in one study being eclipsed by another factor in a different system. An improved understanding of this hierarchical structure would greatly enhance management efforts for these species, since it encourages different human responses under different environmental conditions (Hobbs and Humphries 1995; Mack, Simberloff et al. 2000). Recent studies on everything from corals (De'ath & Fabricius 2000) and fish (Rejwan *et al.* 1999) to reptiles (Andersen *et al.* 2000) have used hierarchical modeling, particularly classification and regression trees, as tools to understand habitat preferences related non-linearly or with complex interactions to species presence and abundance. This approach acknowledges that for many species distribution may not be determined as much by one limiting variable as it is by constrained responses to several variables, often contingent upon each other. To date,

such modeling approaches remain underutilized for investigating species invasion patterns and management possibilities (Hulme 2006).

In many ecosystems, particularly forests and other late-successional communities, age and prior use of the landscape appear to be just such overarching variables, for a number of reasons. First, increasing age greatly increases the potential pool of species that can establish in that community by providing time for propagules to arrive from distant sources (Bellemare, Motzkin et al. 2002; Godefroid, Rucquoij et al. 2005; Hermy and Verheyen 2007), but at the same time also decreases the amount of open habitat available for those species to establish (Goslee, Niering et al. 2005; Fraterrigo, Turner et al. 2006). Several groups working in post-agricultural forests, in both Europe and North America, have demonstrated that species composition of such forests is tightly related to their age, as well as other factors such as distance from source populations (Foster, Swanson et al. 2003; Kolb and Diekmann 2004; Flinn, Vellend et al. 2005; Fraterrigo, Turner et al. 2006; Chauchard 2007). Persistent seed banks can also play a large role in repopulating young forests, but their importance tends to diminish with increasing time in agriculture, especially when active cultivation occurred (Bossuyt and Hermy 2001). Disturbance-tolerant species tend to be smaller components of older systems than younger ones *sensu* Davis *et al.* (2000), although most mature systems also contain small areas of more recent disturbance.

A second important interaction of prior use with contemporary plant communities is mediated through legacies of soil alteration and amendment. The majority of secondary, post-agricultural forests have less soil carbon and higher levels of phosphorus

than neighboring non-farmed forests, while at the same time also exhibiting higher N mineralization rates (Fraterrigo, Turner et al. 2005; Falkengren-Grerup, ten Brink et al. 2006; Flinn and Marks 2007). Also, changes in the soil microbiota can persist for years after abandonment, with a general trend toward lower fungal and higher bacterial biomass in younger forests (Fraterrigo, Balser et al. 2006). Exact differences in soil properties will vary depending on the nature and duration of the prior agricultural land use (McLauchlan 2006). Coupled with the biotic conditions of younger forests, especially relatively high light availability, these altered soils tend to favor plant species with high rates of growth and reproduction and low specificity for particular soil symbiotes (Vanwalleghe, Verheyen et al. 2004; Neill, Von Holle et al. 2007). These are all traits that are well-documented to be predominant among invasive species.

Third, in most ecosystems age of the system is tightly correlated to a number of physio- and topographic variables that determine the ease of human development and alteration on that portion of the landscape. For instance, old prairie remnants may persist on pockets of soil that were too dry for agriculture or old forests may be found on the steepest and most inaccessible portions of mountain slopes (Gerhardt and Foster 2002; Taverna, Urban et al. 2005). Lewis *et al.* (2006) here draw the useful distinction between direct and indirect legacies, where alterations present because of land use itself (such as of soil, above) create direct legacies, and those differences due to landscape characteristics that shaped human decisions about land use create indirect legacies. In both cases, the legacies of human land use decisions affect the structure and composition of plant communities, apparently for very long time scales. Recent work has found the sites of ancient Roman homesteads in France to possess different plant communities from

surrounding forestland that had not been as directly affected 1800 years before (Dambrine, Dupouey et al. 2007). In an entirely different climate and biome, the legacies of ancient land use and soil erosion can still be seen in the plant communities of contemporary Guatemala (Beach 1998). In short, because it encompasses a range of biotic and abiotic variables, knowledge of a system's age and land use history can be a powerful tool to better understand the biological community thereon.

Recently, several studies have begun to elucidate the relationship of age and land use history to plant invasion processes. Much of this work has focused on early successional and frequently disturbed habitats (i.e.- roadsides and riparian areas), though, leaving uncertain the role of community age and history in influencing plant invasions in later successional habitats. In terms of invasive species richness, frequent disturbance and the proportion of early successional habitat within the landscape both increase susceptibility to invasion (Pauchard and Alaback 2004; Hill, Tung et al. 2005; Parks, Radosевич et al. 2005; Johnson, Litvaitis et al. 2006). But the abundance of individual species also appears to be influenced by age and history, even in later successional stages. For example, the abundance of several invasive woody species decreases with increasing forest stand age (Lundgren, Small et al. 2004; Flory and Clay 2006). Aragon and Morales (2003) described a similar trend, with the additional finding that invasive richness was highest around towns and other settlements. One recent study (DeGasperis and Motzkin 2007) attempted to more clearly link history and invasion for *Berberis thunbergii* in the northeastern U.S., arguing that at the time of its initial invasion, invasible habitat was more prevalent than is true now, allowing the species to establish and persist even as afforestation continued. These studies point out some clear trends, but more work needs

to be done to confirm their general applicability, particularly for herbaceous and annual invaders.

In forested ecosystems of the eastern U.S., one important invader is *Microstegium vimineum* [Trin.] A. Camus (hereafter *M. vimineum* or stiltgrass), which was first recorded in the country in Knoxville, TN in 1919 (Fairbrothers and Gray 1972), and has been rapidly expanding its range in recent decades. It is an annual, C₄ grass that does extremely well in riparian areas, roadsides, field margins and other habitats with frequent disturbance (Barden 1987; Redman 1995). The species has also demonstrated the ability to invade the herbaceous layer of minimally-disturbed forests, however, and as such is a growing concern for the threat it poses to native herb diversity (Belote, Weltzin et al. 2004; Leicht, Silander et al. 2005; Belote and Weltzin 2006; Judge 2006). It appears to be primarily dispersed through floating or being carried along with mud on feet or fur of passing animals (Peskin 2005; Morrison, Lubchansky et al. 2007), methods which allow for potentially widespread dispersal. Vehicles can also carry the seeds incidentally along roadways (Peskin 2005). Several studies have shown that stiltgrass is ultimately limited by canopy shade which reduces light to 3-5% of full sunlight (Gibson, Spyreas et al. 2002; Cole and Weltzin 2005), but this is a level of shading not achieved in many forests, especially under young hardwood canopies.

Since it is an annual plant dependent on seed production rather than clonal growth for population expansion (Gibson, Spyreas et al. 2002; Cheplick 2005), and thus not subject to biomass subsidization by parent ramets, *M. vimineum* is an ideal plant for studying local biological constraints on population establishment and expansion

(Claridge and Franklin 2002; Cheplick 2006). In addition, since the species was expanding within the North American landscape at the same time as many formerly agricultural fields were slowly returning to forest cover (mid-20th century) (Foster 1992; Luce 2001), it is possible to examine the importance of forest age to the invasion process. Forest age itself is tightly linked to other landscape variables such as topography, soil types and woody plant composition/density (Bellemare, Motzkin et al. 2002), variables which are all important to the spread and establishment of *M. vimineum* (Cole and Weltzin 2004). For instance, formerly agricultural soils can retain a legacy of higher nutrient availability (Compton, Boone et al. 2000; Hill, Tung et al. 2005), a factor which favors growth of *M. vimineum* (Vidra, Shear et al. 2006). At the same time, in many areas native shrub communities return more slowly to young forests than invasive species (Glitzenstein, Canham et al. 1990; Aragon and Morales 2003), and thus are not as able to exclude invasion through light competition.

I examined a suite of such factors that have been previously found to be individually important for *M. vimineum*, within a landscape in which this species occurs in patches of various size and density across a wide range of environmental conditions. I hypothesized that different sets of controls may operate on previously-farmed vs. previously-wooded land, and that the relative importance of canopy structure, dispersal pathways and soil fertility may vary with topography. I predicted that *M. vimineum* abundance would be lower in (a) conditions of high light competition from adjacent trees and shrubs and in (b) locations with poor soil resources as measured by low organic matter content and/or acidic pH values. In addition, the presence of suitable seed dispersal pathways, namely surface water and animal traffic, should also be necessary to

develop the majority of invasive patches (c). Finally, I expected forest age and prior use to influence all of the above controls, such that their relative importance would shift between old and young stands.

Materials & Methods

Study Area

This study took place in the Sourland Mountain region of west-central New Jersey, USA (approximate coordinates: 40°23'N 74°50'W). The Sourlands are a 28-km long ridge (40-150m in elevation), composed of Triassic-era igneous diabase intruded into the dominantly sedimentary rock terrane of the surrounding Piedmont. The diabase rock weathers slowly, leaving extremely stony soils with abundant large boulders in some landscape positions. At the turn of the 20th century, like much of the eastern U.S., level land in the region was predominantly cropland, whereas steeper and rockier areas were retained as forest lands (Hall, Motzkin et al. 2002). A topographic survey performed by the NJ State Geologist in the late 1880s (Cook and Vermeule 1889) mapped in detail the locations of forested tracts of land and farm field boundaries. In the first half of the twentieth century, as the economics of small-scale farming changed, much of the region's population left, creating a mosaic of old secondary forests and young forests growing over old fields and pastures of various ages (Foster 1992). This trend accelerated after World War II, leaving a predominantly forested landscape by the 1960s (Luce 2001; Banisch Associates 2004). Recent changes in the region have included encroaching suburban development and traprock (diabase) quarrying.

Sampling Design

Information on current and historical locations of forests in the area was obtained from aerial photographs archived by the NJ Department of Environmental Protection (Trenton, NJ) and processed using ArcMap. Orthophotographs from 2002 (1' resolution) were used for contemporary conditions as they represented the most recent photography available at the time of the study. The earliest photos of the region are from the mid 1930s, and have been hand-mosaicked to produce a composite image (6.5' resolution). These two sets were then viewed in comparison under the same projection to locate stands present before and after circa 1935. Photos from the intervening decades (taken every 7-10 years) were manually examined to more accurately establish the age and prior land use of forests that regenerated after the 1930s. The digitized Cook/Vermeule map (Rutgers Center for Remote Sensing and Spatial Analysis) was used to establish which specific tracts were closed-canopy forest in 1890. Specific study sites were selected to span the length of the region, and in all cases paired a young stand (≤ 70 yrs. old; pasture/old field or crop field in 1930) with an adjacent old stand (≥ 80 yrs. old; closed canopy by 1930, also present as far back as the Cook/Vermeule study in 1890) (Fig. 1).

Within each stand selected for the study (20 total), circular plots (5m radius) were surveyed along radial transects from the stand center, running out in eight directions along the N-S, NE-SW, E-W and SE-NW axes (Fig. 2). For the five largest stands, plots were spaced every 50m along the transects, but the majority of plots were

spaced 25m apart. The average number of plots surveyed per stand was 62, with a minimum of 40 and a maximum of 105 in the largest stand. A total of 1248 plots were surveyed in the summer of 2006, 558 in young stands and 690 in old stands.

The percent cover of *M. vimineum* present was visually estimated within each plot in cover classes with the following medians: 0, 0.05 (one to several plants), 0.5, 3, 7.5, 12.5, 17.5, 22.5, 30, 42.5, 60 and 85%. In addition to stiltgrass cover, the percentage cover of understory shrub species was estimated, and the three dominant tree species providing canopy over the plot were noted in descending order, based on their size and proximity to the plot. The percentage of canopy closure was determined using a spherical densiometer, and averaging four readings taken from each plot (each 1.5m from plot center on cardinal directions). I also noted the presence of several potential seed dispersal corridors running in or near ($< 2\text{m}$) each plot, as well as areas likely to represent favorable habitat or points of introduction for the species. Corridors noted included streams, apparent areas of surface water drainage (i.e.-leaf packs or scoured surface), foot trails (human or deer), motorized paths (i.e.- two-tracks), and traces of old trails/roads. Favorable habitat sites and possible introduction points noted were vernal pools and remnants of human land use (stone fences, building foundations, etc.).

The exact position of each plot was determined by either a GPS unit in the field or interpolation from nearby points if dense canopy prevented an in-plot measurement. Data on the slope, aspect, and hillshade (derived algorithmically from the intersection between slope and aspect) of each plot were calculated from 10m-resolution digital elevation models created by the NJ Department of Environmental Protection (Bureau of

Geographic Information Services, Trenton, NJ). Soil series data were derived from the SSURGO databases developed by the USDA-NRCS. The distance of each plot from the current forest edge was determined using an ArcMap script that calculated the shortest line between each plot and the nearest non-forest habitat (agricultural fields, old fields, houses/yards, and open water). The images used for analysis were 2002 aerial orthophotographs, taken by the NJ DEP (Bureau of Geographic Information Services; 1' resolution, 1" = 200'). The distances of old forest plots from forest edges at the time of the earliest photos of the region (mid 1930s; 6.5' resolution) were calculated using the same method with digitized images of these photos. In addition, by inspection of intermediate aerial photos archived by the NJDEP, the approximate age of the forest above each plot could be determined to the nearest decade, from 40 years old to >90 years, based on when forest regeneration was first photographed.

Soil Collection and Analysis

In the summer of 2007, 286 plots (174 old, 112 young) in four stands (2 old and 2 young) were revisited at the northernmost end of the range (Sourland Mountain Preserve). Approximately 50g of soil were collected from the top 5cm of mineral soil in each plot by pooling 3-4 subsamples taken at random points within the plot. These samples were then analyzed for pH and organic matter. pH was analyzed by mixing a 3g portion of soil with 15ml of deionized water, shaking for 5 minutes, and measuring the slurry with a probe (Denver Instruments UP-5) after it had been allowed to settle for 10 minutes. Organic matter was measured as the percent of mass loss-on-ignition (%LOI),

where a sample of known mass was dried for 2 days in a 105°C oven, then fired in a 550°C muffle furnace for 12 hours, and finally re-weighed.

Data on *M. vimineum* presence and abundance in relation to these variables was primarily analyzed using SAS v9.1. Correlations between quantitative and ordinal independent variables were checked using PROC CORR and PROC FREQ, respectively, and multicollinearity was calculated using the ‘vif’ and ‘tol’ options (PROC REG) on a linear regression of those same independent variables (age, canopy cover, native shrub cover, slope, distance-to-edge, hillshade and dispersal pathways). No variables were found to inflate the variance by a factor of more than 1.22, thus the skewing effects of multicollinearity on logistic regressions were considered negligible in this study. Paired t-tests were used to compare means of independent variables in the plots of adjacent old and young stands. PROC REG and PROC GLM were both used to examine the effect of individual variables, crossed with the effect of age, at the plot-level. These analyses used raw values or means based on the entire range of cover classes listed above. For the ANOVAs, differences in means between groups were always tested using Tukey’s honestly-significant-difference.

PROC LOGISTIC was used to construct logistic regression models of plot-level variables, and verified using Wald maximum-likelihood values. Several models were constructed to test effects of variables on both presence/absence and abundance of invasion. For the latter, *M. vimineum* cover was classified into five invasion categories (None [0%], Incipient [0.05-5%], Low [6-25%], Moderate [26-50%], and High [51-100%]). For both models, I expected to see increased canopy cover (trees and shrubs),

distance to the forest edge, and forest age decrease the abundance of *M. vimineum*, while the presence of dispersal pathways would increase the species' abundance. A similar model was constructed for the 286 plots revisited in 2007, with the addition of pH and SOM, which I expected would both inhibit *M. vimineum* as they increased. Also, PROC CATMOD was used to compare invasion presence among plots that differed along several categorical variables: age (young vs. old), pathways (none vs. some) and aspect (N,S,E,W). The initial model found aspect to be non-significant, so it was discarded in the final model, which included age, pathways, and their interaction.

Finally, classification-and-regression tree (CART) algorithms on all 1248 plots were run using R (v 2.6.0). The analysis weighed the following independent variables against *M. vimineum* presence/absence: pH, organic matter, slope, aspect, hillshade, soil series classification, edge distance (2002), plot age, prior use, dispersal pathways, tree canopy density and native shrub cover (%). The same variables were then used in a model to assess abundance. The package 'tree' was used to run the analysis, with the original tree being pruned after cross-validation to include branches with the lowest deviance without sacrificing explanatory power.

Results

General Plot Trends

The stands selected for study encompassed a diverse set of hardwood forests (Table 1). Overall, *M. vimineum* occurred in nearly 77% of the plots, and is a substantial

component of the herbaceous layer in many of those plots, with a mean cover of 14.3% ($\pm 0.7\%$; Table 5). With a median of only 3% cover, however, the distribution is strongly right-skewed. A check of the Pearson correlation coefficients among the variables collected in this study shows that age and distance-to-edge (2002) are each correlated with several other variables (Table 6). Since distance-to-edge is directly dependent on stand age, its correlative significance is simply a reflection of older stands having larger distances-to-edge. Native shrub cover is also weakly correlated to several variables, although the large sample size reduces the absolute strength of those relationships. Testing tolerance and variance inflation factors (VIF) for each of these quantitative variables revealed that despite the Pearson correlations, none of the variables significantly alter the interpretation of logistic regression results. As expected, the highest VIFs were for distance-to-edge and age, but both were quite weak as inflators, with an approximate factor of 1.2. In short, because of the large sample size and high variability among plots, the correlation of age to other variables, although significant, is not strong enough to affect model interpretation.

In order to confirm the ecological differences between adjacent old and young stands, t-tests were used to compare means of their plots for independent variables. Eight out of ten pairs had significant differences in mean slope at $\alpha = 0.05$, with young stands on gentler slopes than their old neighbor. Because of that, 60% of the pairs had differences in hillshade values. Canopy closure (50% significant) and dispersal pathways (30%), however, were more often equivalent between adjacent stands. Total and invasive shrub cover were higher in most (80%) young stands than in their older neighbors, while native shrub cover was only significant in 60% of cases.

Multiple Logistic Regressions

Simple linear regressions of the independent variables collected against *M. vimineum* cover indicate that this is not an effective way to analyze the patterns. Even variables with a significant regression have very low r^2 values (Table 7). Thus, threshold effects, rather than simple linear relationships, appear to be more relevant for these invasion patterns. In a logistic regression model including plot age, pathway presence, canopy density, native shrub cover, slope, hillshade and distance-to-edge, as well as the interactions of each variable with age, age and canopy were both strong predictors of *M. vimineum* presence across all plots (Table 8). Their interaction was also highly significant, with older forests having patchy canopies much more likely to be invaded than old stands with continuous canopy cover. Hillshade, a secondary variable incorporating both slope and aspect, and thus approximating incident solar radiation, was also a significant regressor for the presence of invasion. None of the other variables were significant. In contrast, running a similar model on the actual abundance of *M. vimineum* (none, incipient, low, moderate, high) reveals that most of the variables are significant (Table 8). Again, age and canopy cover are strongly significant, with the presence of dispersal pathways, native shrub cover and slope also very influential on abundance. The interaction of age with each of these variables is also significant, highlighting the differential effect of each factor in forests of different ages. For instance, dispersal pathways in older forests increase the abundance of stiltgrass much higher relative to isolated older plots than do similar pathways in younger forests, while pockets of high native shrub cover in younger stands have a much more inhibitive effect on stiltgrass relative to other young stands than do such areas in older stands.

Age

The strong influence of forest age on *M. vimineum* invasion becomes apparent when comparing the mean stiltgrass cover of plots under different age stands (Fig. 11a). The youngest forests have mean cover nearly four times as high as those stands older than 80 years. Further, little statistical difference exists between stands from 40-80 years old, but invasion into forests older than 80 years is dramatically lower. The overall model to compare them was highly significant ($F_{6, 1247} = 47.64, p < 0.0001$). For simple presence/absence of *M. vimineum* the difference is just as notable: 35.9% of old forest plots (> 80 yrs.) remain uninvaded, while only 8.5% of younger plots are without any stiltgrass cover. Prior land use is another method of looking at the effects of age, and a comparison of the land use of the plots in the 1930s reveals a similar pattern (Fig. 11b). Plots that were already closed-canopy forests at that point (i.e.- 80+ years old), had the lowest amount of stiltgrass invasion. Of the younger forests, those that were crop fields in the 1930s had the highest stiltgrass cover, with former hayfields and pastures falling intermediate to the two extremes. A two-way model combining age and prior use and their interactions is highly significant (overall $F_{16, 1247} = 33.9, p < 0.0001$), with the prior use ($F_4 = 8.94$) and age*use interaction ($F_6 = 28.31$) being more significant than age alone ($F_6 = 3.32$).

Canopy Effects

Although tree canopy cover has a strong influence on invasion in both of the above logistic models, a simple linear regression of closed canopy percentage is not as revealing. It is highly significant (slope = -1.11% *M. vimineum* / 1% canopy closure, $F =$

52.84, $p < 0.0001$), but the proportion of variability among plots explained by this variable was very low ($r^2 = 0.0401$). It is worth noting that these plots are poorly differentiated in terms of canopy cover, as all are essentially under closed forest canopies (mean = 95.6% [$\pm 0.1\%$]). In a two-way linear model of canopy and age, both of these variables and their interaction are highly significant in explaining stiltgrass cover (overall $F_{13,1247} = 27.98$, $p < 0.0001$). Again, canopy gaps above older plots promoted stiltgrass invasion relative to plots with no such gaps more than gaps above younger plots relative to other young plots (Fig. 12). Even more than total canopy cover, the species makeup of the tree canopy was strongly correlated with *M. vimineum* abundance. Specifically, *Acer rubrum*- and *Fraxinus americana*-dominated plots had 2-5x more *M. vimineum* cover than plots with any other canopy dominant, with mean cover between 22 and 30% (Fig. 13). By contrast, *Quercus* spp., *Liriodendron*, and *Betula lenta* canopies were all associated with between 5 and 8% cover. Of course, these differences are also partly reflective of the different tree communities in forests of different ages, with *Acer rubrum* and *Fraxinus americana* dominating younger stands in this region. The overall linear model for tree canopy yielded $F_{6, 941} = 39.81$, with $p < 0.0001$.

Shrub layers within plots also played an important role in influencing *M. vimineum* invasion. Although neither exotic nor native shrub cover was significant in the logistic regression for presence of invasion, native shrub cover was influential on the abundance of invasion, and had a different effect in young and old plots. Native shrub cover was negatively correlated with *M. vimineum* abundance in younger forests while it was weakly positively correlated in older stands (Fig. 14). This probably reflects the

relatively higher cover of shrubs under canopy gaps in older forests, which could also allow higher densities of stiltgrass.

The relationship of exotic shrub cover to *M. vimineum* invasion is not at all significant when considering absolute exotic cover. Exotic shrub richness alone (Fig. 15a), however, does show that plots invaded by one or two species had significantly higher *M. vimineum* abundances than other plots with more or fewer invasive species. This likely reflects the very high density of shrub cover that such plots have, which effectively prevents high densities of stiltgrass from persisting. Statistically, plots with 3 or 4 invasive shrub species were not dissimilar in terms of *M. vimineum* to those with no invasive shrubs (Overall GLM $F_{6,1266} = 9.23$, $p < 0.0001$). Again, particular invasive shrub species were differentially associated with the invasive herb (Fig. 15b). Of the possible invasive shrubs present in the region, only three were the dominant shrub by abundance in more than 4% of the plots. Of those, *Rosa multiflora* was clearly associated more strongly with *M. vimineum* than either *Berberis thunbergii* or *Rubus phoenicolasius*, which were not statistically different from those plots with no invasive shrubs present. This yields an overall linear model $F_{3,1141} = 24.43$ and $p < 0.0001$.

Viewed across forest age, an inverse relationship generally exists between shrub abundance and *M. vimineum* success, until reaching the oldest forest ages, when both total shrub and *M. vimineum* cover decline (Fig. 16). This decline is presumably due to high shade levels cast by over- and understory trees in more developed forests. Mean shrub cover increased with forest stand age up to 80 years post-abandonment, after which total shrub cover declined precipitously. Native shrub species cover followed a similar pattern, although with greater interdecadal variation. *M. vimineum* cover showed a

different trend, averaging its highest values in the younger forests then declining notably at 60 yrs., and even more steeply 80 yrs. post-abandonment.

Dispersal Opportunities

The presence of dispersal pathways is very important for *M. vimineum* establishment and success. Although not a significant factor in the presence/absence model, differences among pathways do have a strong influence in the abundance model ($F= 6.141$, $p < 0.0001$), and the interaction between age and pathways is even more significant. The dispersal effect is most clearly revealed when contrasting plots with no obvious dispersal pathway and those adjacent to waterways (Fig. 17). Plots located in or near vernal pools, in particular, had much higher levels of invasion than most other plots. Richer edaphic conditions in these small, temporary pools may partly account for the higher stiltgrass abundance, especially by retaining higher soil moisture later into the growing season. But increased dispersal opportunities during the high water months are also likely to boost invasion, since seeds from even a small patch in one part of the pool can be quickly dispersed by floating over a wide area. The design of this study does not allow for effective differentiation of these effects, but even with vernal systems removed from the model it is still significant ($F= 3.451$, $p= 0.0006$), driven by the difference between plots along streams and those without obvious corridors or along trails.

Plots with upland dispersal pathways, such as along roads and trails, were not statistically different than plots with no obvious pathway. The interaction between forest age and dispersal pathways is even more revealing, with the interaction effect contributing to a highly significant overall model (Fig. 18). Overall, *M. vimineum*

abundance was lower along all pathways in old forests than in young. This age effect is largely negated, however, when the plots are associated with vernal waterways, where the mean extent of invasion is essentially equal between the age categories. Another striking age-driven difference occurs in plots along foot paths or with no obvious pathway. Here, old plots are very minimally invaded, while young plots still have substantial levels of invasion. Finally, although specific pathways make a large difference for old forest plots, note that there is no significant difference among pathway types for young forests.

In the log-linear analysis (PROC CATMOD) of categorical variables *age* (old/young), *pathway presence* (Y/N) and *aspect* (N,S,E,W), only the former two were informative enough to include in a model of *M. vimineum* presence/absence (Table 9a). Overall, the modeled probabilities of stiltgrass presence illustrated the high likelihood of finding the species in young forests (95.2%) as opposed to older stands (75.0%; Table 9b). The importance of pathways for presence in older forests in particular is illustrated by the sharp difference between plots with (82.7%) and without (60.8%) such pathways.

Slope and Hillshade

Topography also affects the abundance of *M. vimineum* among plots. Slope percentage was strongly negatively related ($-0.6456 \% M. vimineum / 1\% \text{ slope}$; $p < 0.0001$) to the abundance of *M. vimineum* at all stands, although there was a high degree of variability among plots ($r^2 = 0.0496$). Broken down categorically, it is clear that much of the significance of slope is due to high levels of *M. vimineum* on the most level sites

(Fig. 19), as densities of stiltgrass were statistically indistinguishable in plots with a slope greater than 5%. In other words, a threshold exists between 5 and 10% slopes, above which invasion is dramatically less extensive, but below which plots with a wide range of stiltgrass abundances can be found. A two-way model using slope category and age was highly significant ($F_{31,1216} = 13.7$, $p < 0.0001$), with age contributing most of the significance, although the interaction effect was also highly significant.

Soil Factors

For the subset of plots that were sampled for soil variables, pH and organic matter were not found to have a significant effect in logistic regression models, although canopy, age, and slope were again influential for this subset. Despite its lack of significance in these models, SOM (which ranged from 6% to 84% in these plots) had a significant regression against absolute *M. vimineum* cover ($m = -0.677\% \text{ } M. \text{ vimineum} / 1\% \text{ SOM increase}$), and explained 13.5% of the variability among these samples. This is due, however, to the confounding of organic matter in these plots with age, slope and stoniness. A number of plots showed organic matter greater than 25%, and were found on very thin soils over boulders where little mineral soil could be present. These rocky plots made up nearly 20% of the subsample, and were mostly on very steep slopes, in the oldest and least accessible portions of the sampled area. Their average *M. vimineum* cover was only 3%, as compared to nearly 25% for the remainder of the subsample on more mineral soils (Fig. 20). Measurements of pH did very little to explain the variability of invasive abundance, even though plots ranged from acidic (near 4) to circumneutral: relatively dense or sparse stands of *M. vimineum* occurred throughout that range.

Underlying soil series does have an effect on *M. vimineum* abundance, especially in younger forests, which have a wider range of soil types. Soils derived from diabase or argillite shale (semi-metamorphic) are much less invaded than those derived from sedimentary rocks. These variables, however, are heavily correlated with forest age and land use, with younger, formerly agricultural forests predominating on sedimentary soils, and continuous forests occurring mainly on igneous and metamorphic uplands.

Hierarchical Models

Results of the classification-and-regression-tree analysis for the entire sample of plots revealed that forest age was the most important determinant of the presence of invasion (Fig. 21). In forest plots younger than 95 years old, over 92% of the plots were invaded to some extent. In older plots, while invasion proportion was still substantial, there was a discernable difference between plots with different amounts of tree canopy closure. Plots under canopies less than 95% closed were invaded 87% of the time, while more heavily shaded plots were only invaded 57% of the time. In these closed canopy plots, the presence of a dispersal vector greatly increased the frequency of invasion. This five node model explains only 20.4% of the overall variability among plots, though.

Similarly, CART analysis shows prior land use to have the most influence on *M. vimineum* abundance, with former fields and pastures being nearly four times more densely invaded than forests present since the 1930s (Fig. 22). Since the land uses are divided between former agricultural lands and former forests, this mirrors the findings

above that age was the single most important factor in determining invasion presence and abundance. Similarly, in older forests canopy closure is the most parsimonious variable, with plots of less than 95.5% closure more heavily invaded than in shadier plots. In contrast, younger forests are next divided by their general soil type, with soils derived from diabase and metamorphic shales (Chalfont, Legore, Mt. Lucas) less invaded than soils derived from shale and sandstone (Lansdale). In the former category, distance from the forest edge became next most important, with more interior plots being less invaded than plots closer to the edges. For the sedimentary soils, prior land use again becomes an important consideration, with former row crop fields showing much higher invasion than those forests on former grasslands. This six-node model explains 35% of the total variability in *M. vimineum* cover among these plots.

Discussion

The factors controlling *M. vimineum* invasion at the level of plant patches are clearly multiple and varied, with relative importances that are contingent upon each other. Forest age was a very strong influence throughout all of the analyses in this study, and appears to be a hierarchically constraining variable, controlling invasion response to a number of other variables. In other words, this landscape appears to be creating a number of indirect legacies, where earlier land use decisions based on topography and soils are tied to current patterns of invasion (Lewis et al. 2006). These other variables are the actual mechanisms whereby *M. vimineum* is limited, although their action will be limited by forest age. Light limitation is clearly a major biotic determinant of success, as is the

case for most forest floor herbaceous species. Other researchers have found the species to be excluded only by light levels as low as 3-4% of full sunlight (Winter, Schmidtt et al. 1982; Gibson, Spyreas et al. 2002; Cheplick 2006), which in most cases is not provided by a tree canopy alone, but overstory trees in conjunction with understory trees and shrubs (Cole and Weltzin 2005). The significance of increasing canopy density in my logistic regression models bears this trend out, even though measurements of photosynthetically-active radiation rather than simple canopy closure would probably strengthen the relationship.

Further evidence for the importance of a dense canopy in excluding *M. vimineum* is seen in the average invasion under various tree and shrub species. In eastern temperate forests, *Fagus grandifolia* is among the deciduous trees which cast the densest shade (Cowell and Hayes 2007), and, not surprisingly, it most effectively excluded *M. vimineum* in this study. The other tree species that were associated with lower levels of invasion (*Quercus* spp., *Liriodendron tulipifera*, *Betula lenta*, *Carya* spp.) do not create such dense shade, but often compose older secondary forests with more developed shrub canopies. On the other extreme, *Acer rubrum* and *Fraxinus americana* forests in this study were often younger, and possessed minimal shrub layers to further attenuate the sunlight reaching the herb layer. Even though these species are often predominant in wetland areas, the small size of the vernal wetlands in this study allowed for an association with a variety of tree species. Thus, the correlation of trees with edaphic factors that might promote invasion is not large enough to influence the distribution of stiltgrass more than age and canopy structure.

A similar relationship between forest age, species composition, and *M. vimineum* invasion can be seen with non-native invasive shrub species. Shrub canopies of *Rosa multiflora* were associated with the densest patches of *M. vimineum*, again because of a combination of *Rosa*'s often open canopy in forest settings and its preponderance in younger forests (Meiners, Pickett et al. 2002; Meiners 2007). *Berberis thunbergii* and *Rubus phoenicolasius*, on the other hand, are more often found in slightly older forests (Webb, Dwyer et al. 2000; Lundgren, Small et al. 2004), particularly where browsing or other disturbances have removed the native shrub canopy. *B. thunbergii* also casts denser shade, and so *M. vimineum* is not as abundant where the shrub is. For similar reasons, plots with higher exotic shrub richness (> 2 spp.) tended to be associated with lower levels of *M. vimineum*, as such plots often have a dense shrub layer to limit light reaching the forest floor (Von Holle and Motzkin 2007).

The role of soil condition in influencing *M. vimineum* success is less clear. I expected to see more invasive success in richer soils where both pH and organic matter were moderate. In addition, previous work has shown that *M. vimineum* tends to create soil-plant feedbacks that raise pH (Ehrenfeld, Kourtev et al. 2001; Kourtev, Ehrenfeld et al. 2003). As expected, plots in this study with high organic matter tended to have very low levels of invasion, but there was no further relationship with invasion at lower levels of SOM. Likewise, there was no clear relationship between invasion and pH in this study. If these relationships are significant for stiltgrass invasion, collection of the data at more sites might further clarify them. Many of the high OM plots in this sample are from extremely rocky areas with only small pockets of soil, and thus are skewed to very high percentages of organic matter. Sampling from a broader range of habitats might help to

alleviate this problem. Alternatively, soil conditions may not determine whether *M. vimineum* can establish and spread in an area, but may influence growth and reproduction. Since this study measured only areal extent of invasion in each plot, rather than aboveground biomass or similar indices of productivity, it is not well-suited to capture such an effect.

Finally, it is clear from both individual linear models and the CART analysis that dispersal pathways have a large influence on *M. vimineum* spread, since they directly control propagule pressure and introduction into new areas. The species may be quite hydrochorous, judging from habitat preferences in its native and invasive ranges (Barden 1987; Scholz and Byfield 2000; Luken and Spath 2002). The proclivity to follow roads and trails is also not surprising, since it has been shown to use these as pathways in other studies (Peskin 2005). What is perhaps unexpected is that historic human land uses still leave a perceptible influence on stiltgrass abundance, and are just as pronounced in their effects as contemporary roads and trails. Considering that most of the historic landscape elements seen in this study were abandoned 40-80 years ago, the clear signature of their presence is intriguing. Such elements do represent possible sites of introduction, and mostly occur in areas where native plants have faced continual pressures in the succeeding decades from exotic shrub competition and deer herbivory (Pedersen and Wallis 2004; Griggs, Rock et al. 2006). The location of such sites on former agricultural lands also entails many of the legacy effects discussed above, such as enriched soils (Compton *et al.* 2000) and depauperate woody plant communities (Bellemare *et al.* 2002). These variables also contribute to invasion success.

It's also important to note that even plots with no obvious dispersal pathway present, which made up the majority of the plots, sometimes had substantial levels of invasion. This is likely due primarily to the short-distance dispersal of seeds from parent patches as plants fall over and decompose (approx. 1m/yr). Over a number of years, this could add up to a large degree of population expansion, and the species has been in the region for at least 60 years. In addition, the idiosyncratic movement of deer and other mammals through forests with seeds in their fur or lodged in their hooves, or even in passage through their guts (Pakeman, Digneffe et al. 2002), could potentially be responsible for dispersal at sites away from more obvious sources. Indeed, the widespread distribution of *M. vimineum* in this landscape is likely responsible for the low percentage of overall variability explained in both the logistic and CART models. Enough time has passed since initial introduction to the region to allow stochastic movement of the seed through the landscape, and thus obscure some of the initial causal factors. It appears that as populations approach equilibrium in the landscape they are more widely distributed than any of their individual predictor variables.

In sum, forest age is the single most important variable in understanding *M. vimineum* invasion, in large part because it encapsulates many other variables that influence either seed dispersal and introduction (i.e.- slope, pathways) or establishment and growth (i.e.- tree and shrub canopies, soil richness). This finding is in accord with a growing body of research illustrating the strong correlation between land use history and plant invasions (Lundgren, Small et al. 2004; Pauchard and Alaback 2004; Von Holle and Motzkin 2007), but most of these studies have so far focused on overall exotic richness, and generally focus more on woody invaders. Thus, it is revealing to see this same

phenomenon occurring for an herbaceous invader. Furthermore, different factors affect invasion depending on the age of the forest, indicating that a hierarchical structure may be at work in controlling the pattern of invasion. Namely, canopy cover was the most important variable in older forests, with canopy gaps encouraging higher abundance of stiltgrass relative to closed canopies. For young forests, several variables are crucial, particularly soil type and shrub canopies. An understanding of these age-correlated variables across an entire landscape can help to account for the widespread distribution of this invasive species, and reveals that plant invasions can be constrained by a hierarchical arrangement of limiting factors, rather than by just one primary variable.

Table 5. Summary table of independent quantitative variables present at all 1248 plots surveyed in '06. Means are presented $\pm$ 1 s.e.

	<i>M. vimineum</i> %	Native Shrub %	Total Shrub %	Canopy Closure (%)	Plot Age (yrs)	Distance-to- Edge (2002, m)	Slope (%)
Mean (s.e.)	14.3 (0.7)	10.3 (0.4)	25.1 (0.7)	95.6 (0.1)	85 (0.6)	242.3 (4.2)	8.2 (0.2)
Median	3	4	17.9	96.6	100	217.4	5.6
Minimum	0	0	0	37.6	40	4.9	0
Maximum	85	85	102	100.0	100	661.3	77.9

Table 6. Displays Pearson correlation coefficients between important and representative quantitative independent variables influencing *M. vimineum* abundance across 1248 plots.

	Age	Slope	Hillshade	Distance- to-Edge	Dispersal Pathways	Native Shrubs	Tree Canopy
Age	1.000	0.285**	-0.026	0.301**	-0.116**	-0.074*	0.099**
Slope		1.000	-0.070*	0.175**	-0.043	-0.081*	0.001
Hillshade			1.000	-0.289**	-0.018	-0.067*	-0.021
Distance- to-Edge				1.000	-0.019	-0.032	0.016
Dispersal Pathways					1.000	0.077*	-0.025
Native Shrubs						1.000	-0.084*
Tree Canopy							1.000

* = significant at $\alpha < 0.05$ ** = significant at $\alpha < 0.001$

Table 7. Simple linear regressions of independent variables collected at the plot scale against *M. vimineum* cover. Boldfaced values indicate those variables that were significant in the logistic regression models.

Dependent	Independent	Overall Sig.	b	r^2	Old Sig.	b	r^2	Young Sig.	b	r^2
Plot <i>M.v.</i> Cover	Plot Slope	***	-0.646	0.05	ns	-0.124	0.005	***	-0.953	0.065
	Hillshade	ns	0.013	0.000	ns	-0.001	0.000	*	-0.217	0.01
	Distance-to- Edge (2002)	***	-0.019	0.015	ns	0.003	0.001	ns	-0.011	0.002
	Distance-to- Edge (1930s)	n/a	n/a	n/a	ns	0.005	0.002	n/a	n/a	n/a
	Plot Age	***	-0.484	0.172	n/a	n/a	n/a	***	-0.372	0.045
	Canopy Closure	***	-1.093	0.039	***	-1.325	0.079	**	-0.589	0.012
	Native Shrub Cover	*	-0.092	0.004	ns	0.013	0.000	***	-0.279	0.027
	Exotic Shrub Cover	ns	-0.019	0.000	ns	-0.004	0.000	***	-0.345	0.064
	Total Shrub Cover	ns	-0.046	0.002	ns	0.004	0.000	***	-0.339	0.096

Table 8. Logistic regression results for variables present at all 1248 plots surveyed in 2006. Results shown are derived from a Wald maximum likelihood analysis, first using a binary model of presence/absence, and then using a stepped model of invasion abundance (none, incipient, low, moderate and high).

Binary Invasion Model			Stepped Invasion Model		
	Wald χ^2	$p > \chi^2$		Wald χ^2	$p > \chi^2$
(Intercept)	25.403	<0.0001	(Intercept)	33.850	<0.0001
Age*Canopy	51.610	<0.0001	Age*Canopy	43.047	<0.0001
Age	44.370	<0.0001	Age	30.035	<0.0001
Canopy	39.096	<0.0001	Age*Pathways	25.070	<0.0001
Hillshade	6.811	0.0091	Canopy	17.888	<0.0001
			Pathways	7.872	0.0050
			Native Shrubs	7.500	0.0062
			Slope	6.805	0.0091
			Age*Shrubs	5.912	0.0150
			Age*Slope	4.560	0.0327

Table 9. Results of a log-linear modeling analysis of the effect of age and pathway presence on *M. vimineum* presence. (a) Estimate and significance values for each variable. (b) Modeled probabilities of *M. vimineum* invasion in a variety of plot types (old vs. young, no pathways vs. one or more (some), and each combination thereof).

(a)

	<i>df</i>	Estimate	Wald χ^2	$p < \chi^2$
(Intercept)	1	0.8513	8775.53	<.0001
Age	1	-0.1009 (Old)	123.21	<.0001
Pathways	1	-0.0761 (None)	70.13	<.0001
Age*Pathways	1	-0.0664 (O,N)	53.41	<.0001
Residuals	12	----	15.38	0.2211

(b)

Overall	Old	Young	None	Some	O/N	O/S	Y/N	Y/S
0.8513	0.7504	0.9522	0.7752	0.9274	0.6079	0.8265	0.8761	1.0000

Figure 11. The relationship of forest age **(a)** and specific prior land uses **(b)** to cover of invasive *M. vimineum*. Categories with different letter labels in each graph are significantly different from each other at $\alpha = 0.05$ (Tukey's HSD). Bars indicate one standard error, and numbers in each column show the number of plots surveyed in each category.

Figure 12. Simple regressions of *M. vimineum* cover against tree canopy closure for both young (<80 yrs. old) and old (≥ 80 yrs.) forest plots. The regression line for young plots is solid; that for old plots is dashed.

Figure 13. Mean *M. vimineum* cover under plots with various tree species as the dominant member of the canopy over each plot. Tree species dominant in less than 4% of the plots are not shown. Bars represent standard error, and species with different letter labels were significantly different at $\alpha = 0.05$ (Tukey's HSD). Number in each column is the number of plots with that dominant tree. 'FAGR' = *Fagus grandifolia*, 'BELE' = *Betula lenta*, 'QURU' = *Quercus rubra*, 'LITU' = *Liriodendron tulipifera*, 'QUAL' = *Quercus alba*, 'FRAM' = *Fraxinus americana*, 'ACRU' = *Acer rubrum*.

Figure 14. Simple regressions of *M. vimineum* cover against native shrub cover for both young (<80 yrs. old) and old (≥ 80 yrs.) forest plots. The regression line for young plots is solid; that for old plots is dashed.

Figure 15. The association of *M. vimineum* with non-native invasive shrub species in the same plot. Exotic shrub richness compared against mean *M. vimineum* abundance is shown in part (a), and specific shrub species are compared in part (b). In part (b), only shrub species dominant in over 4% of the total plots are shown. Bars represent standard error, and species with different letter labels were significantly different at $\alpha = 0.05$ (Tukey's HSD). Number in each column is the number of plots in that particular category. 'RUPH' = *Rubus phoenicolasius*, 'BETH' = *Berberis thunbergii*, 'ROMU' = *Rosa multiflora*.

Figure 16. Changes in native and total shrub cover across forest plots of different ages in the Sourlands, as well as in *M. vimineum* cover. Bars indicate standard error.

Figure 17. Mean *M. vimineum* cover of plots by dispersal pathway category. Bars indicate standard error, and columns identified with the same letter are statistically similar at $\alpha = 0.05$. 'Vernal' = vernal pools/swamps; 'Historic' includes any sign of historic human use, such as old stone fences, inactive pathways or homestead sites. Of 1248 total plots in this analysis, 918 had no obvious pathway, and the other 330 were roughly divided among the other pathway types.

Figure 18. Mean *M. vimineum* cover of plots by dispersal pathway category, and segregated by *a priori* categories of ‘Old’ and ‘Young’ stands. Bars indicate standard error, and columns identified with the same letter within each age class are statistically similar at $\alpha = 0.05$. ‘Vernal’ = vernal pools/swamps; ‘Historic’ includes any sign of historic human use, such as old stone fences, inactive pathways or homestead sites.

Figure 19. *M. vimineum* invasion in plots with varying degrees of slope. Categories with different letter labels in each graph are significantly different from each other at $\alpha = 0.05$ (Tukey’s HSD). Bars indicate one standard error, and numbers in each column show the number of plots surveyed in each category.

Figure 20. Relationship of plot soil organic matter to invasive *M. vimineum* cover in a subsample of 286 plots surveyed in 2007. The dashed line indicates %LOI = 30%.

Figure 21. Classification-and-regression tree results for the presence/absence of invasion at all plots. In each case, percentage of plots invaded under each condition is the response variable, and is in boldface type. Each node is distinguished by an independent variable used in the algorithm, and shows the breakpoint in the quantitative distribution of that variable which most distinguishes the level of invasion, or divides categorical variables into similar groups. Each node also displays the number of observations in that category, as well as the percent of variation among all plots explained by that node. The model explains 20.4% of the overall variance in stiltgrass presence among plots.

Figure 22. Classification-and-regression tree results for the abundance of stiltgrass at 1247 sampled plots. In all cases, mean percent cover of *M. vimineum* by plot is the response variable, and is boldface. Each node is distinguished by an independent variable used in the algorithm, and shows the breakpoint in the quantitative distribution of that variable which most distinguishes the level of invasion, or divides categorical variables into similar groups. Each node also displays the mean *M. vimineum* cover for that group, then the number of observations in that category, and finally the percent of variation among all plots explained by that node. Total deviance explained by this model is 35%.

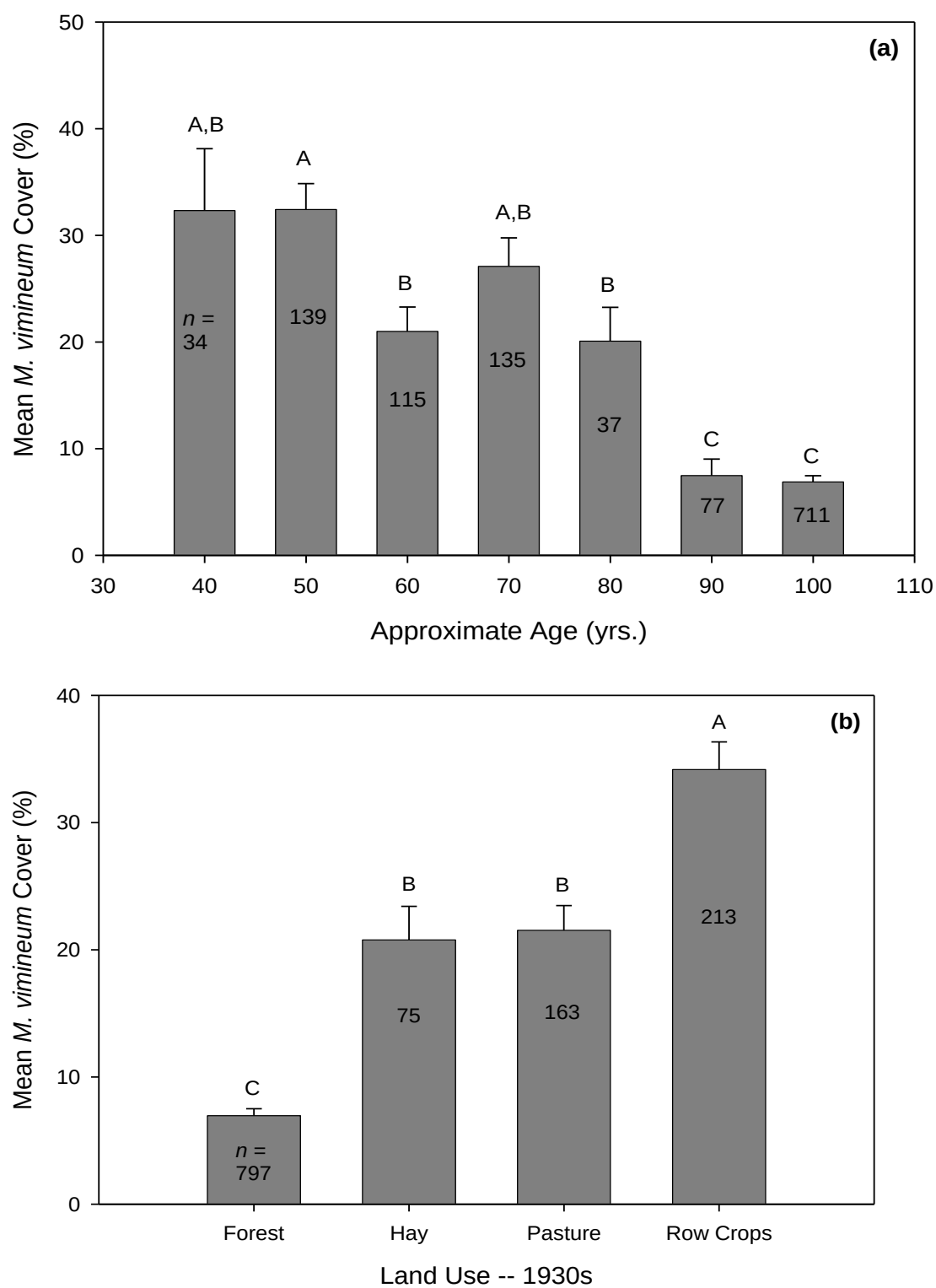
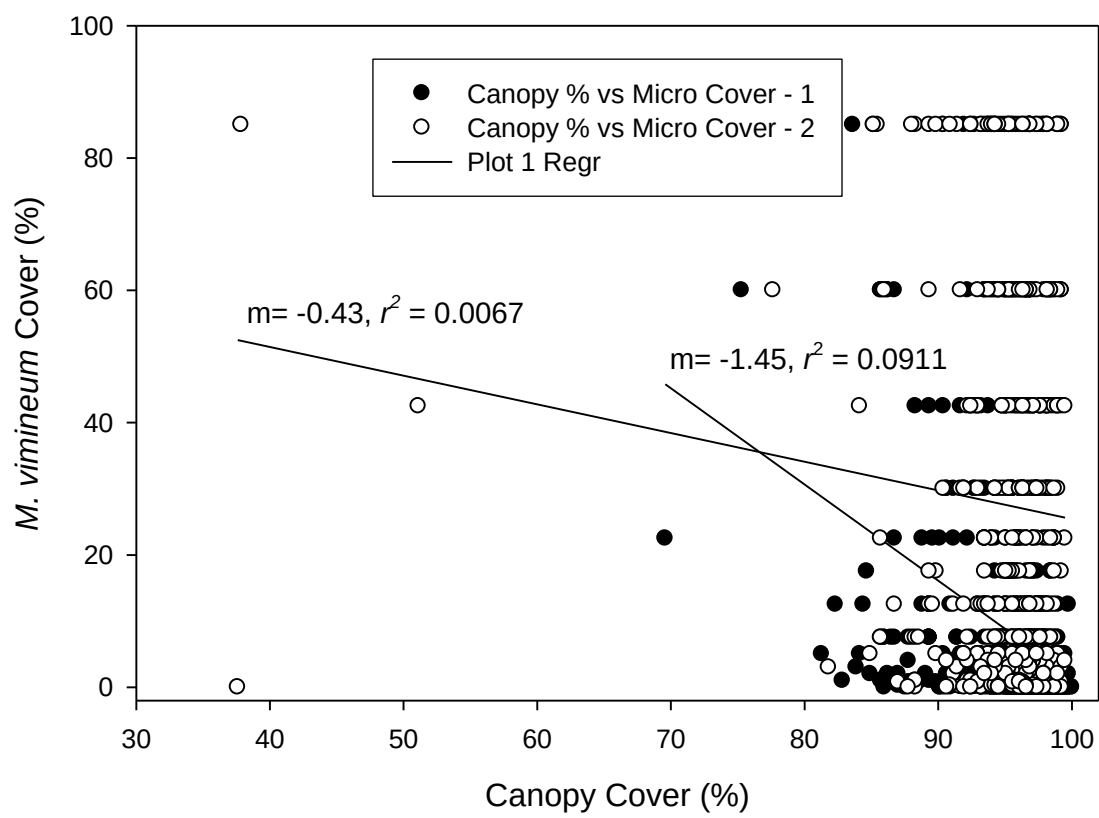


Figure 11

**Figure 12**

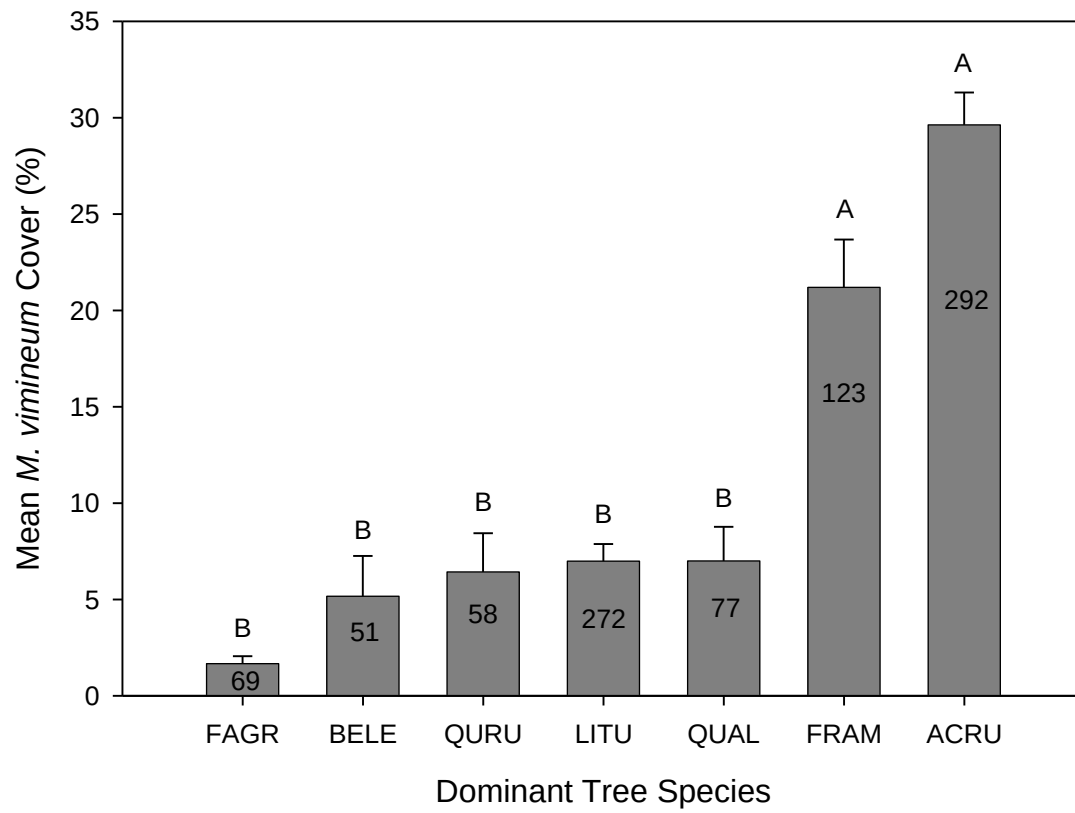


Figure 13

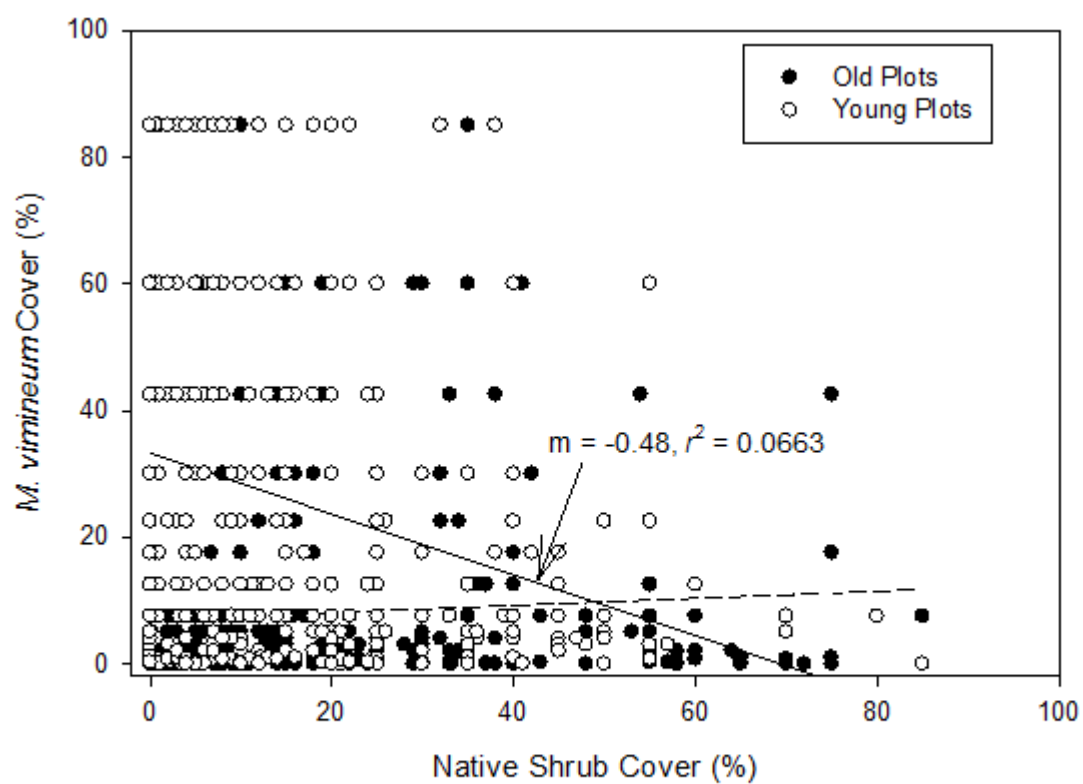
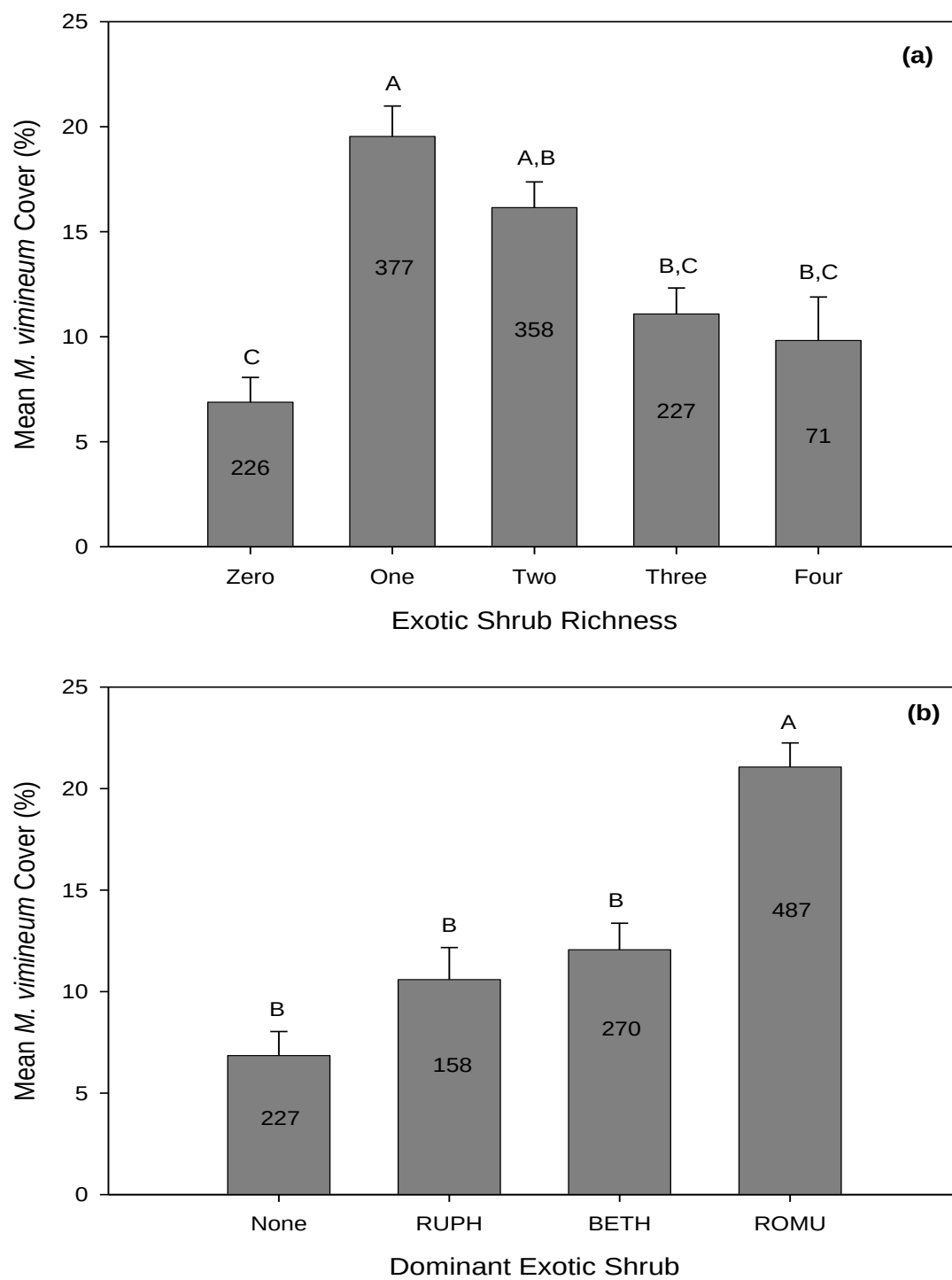
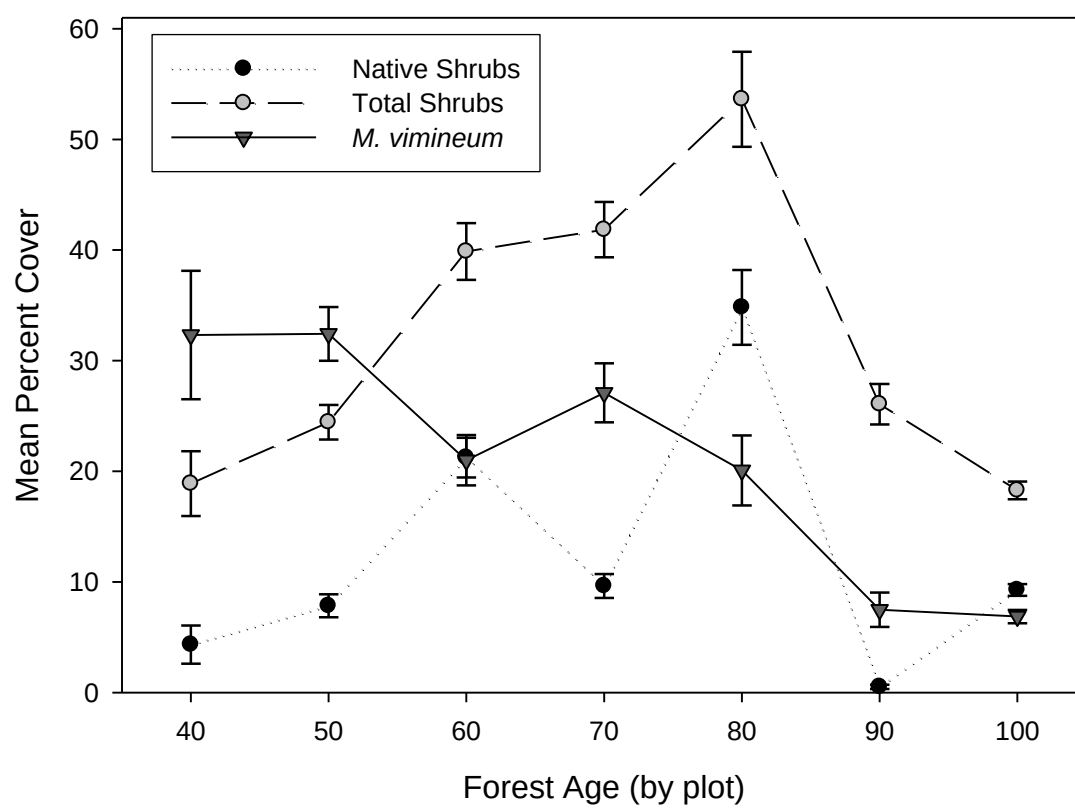


Figure 14

**Figure 15**

**Figure 16**

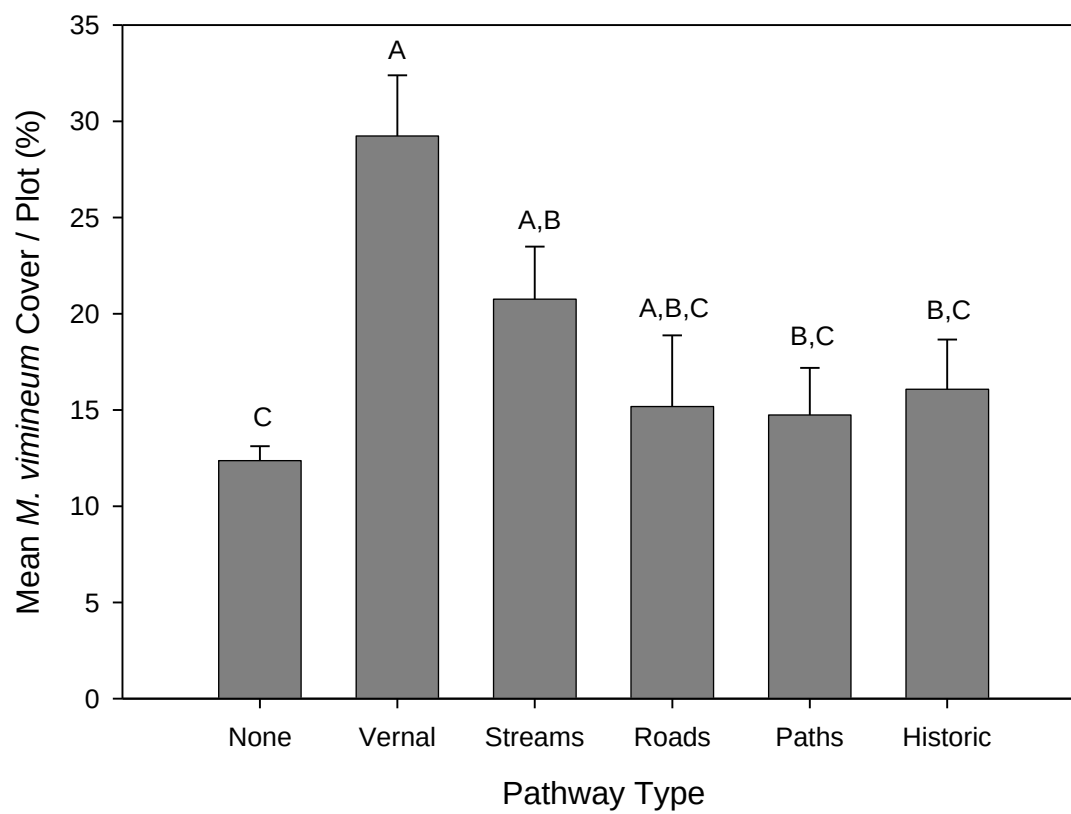


Figure 17

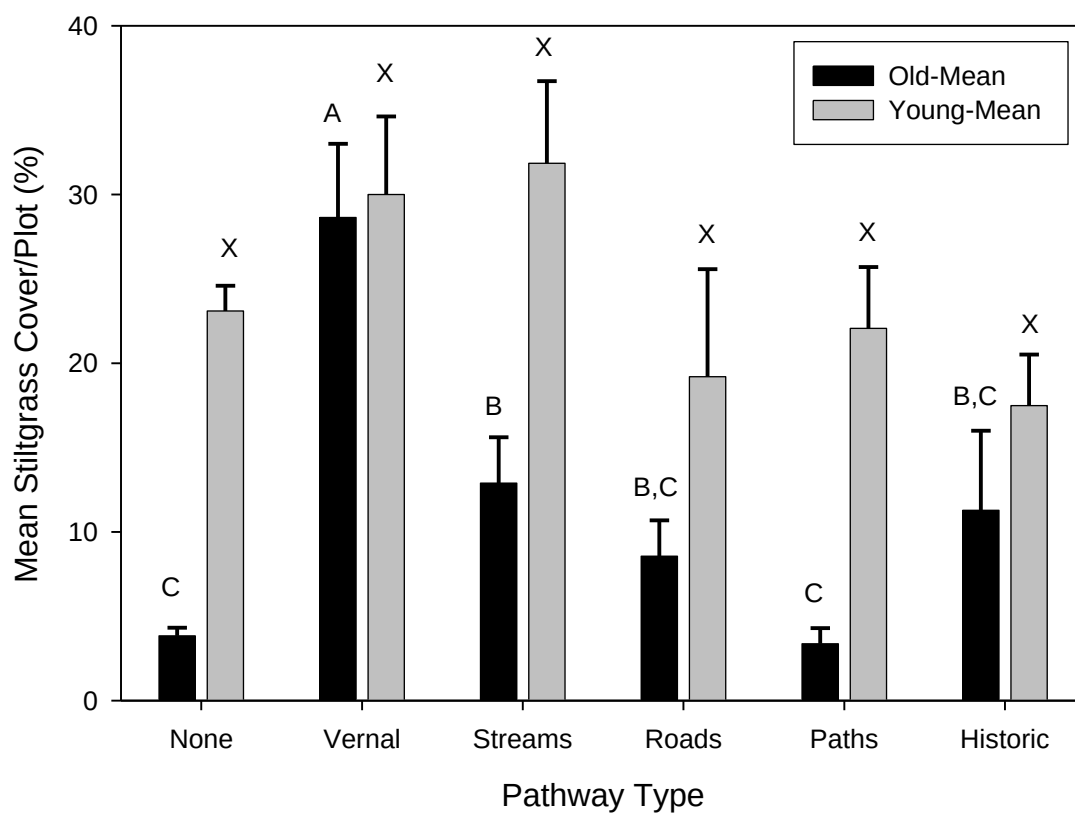


Figure 18

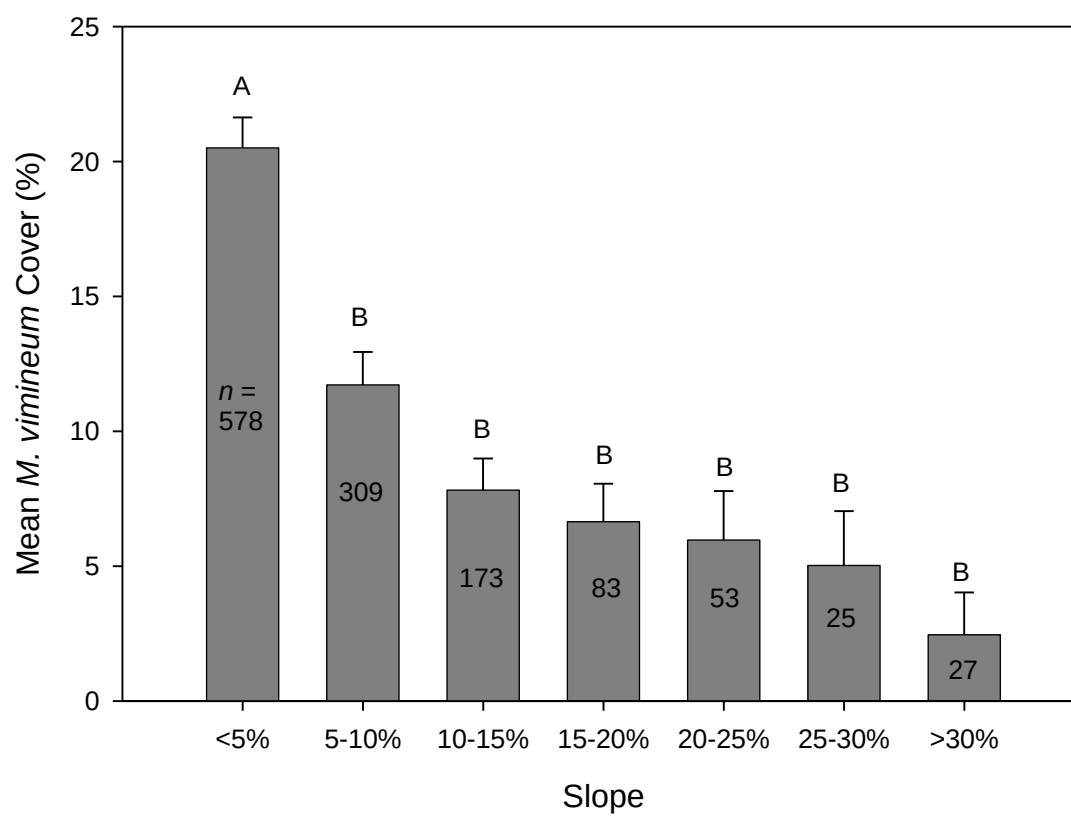


Figure 19

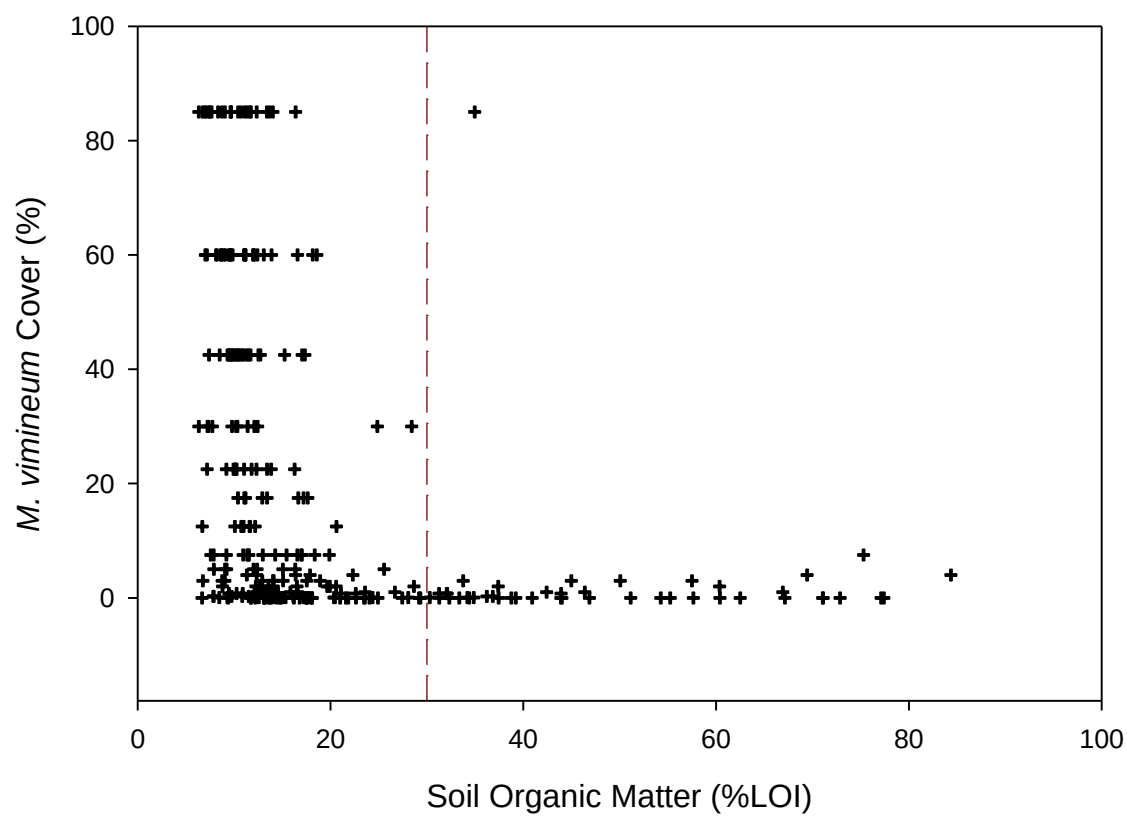


Figure 20

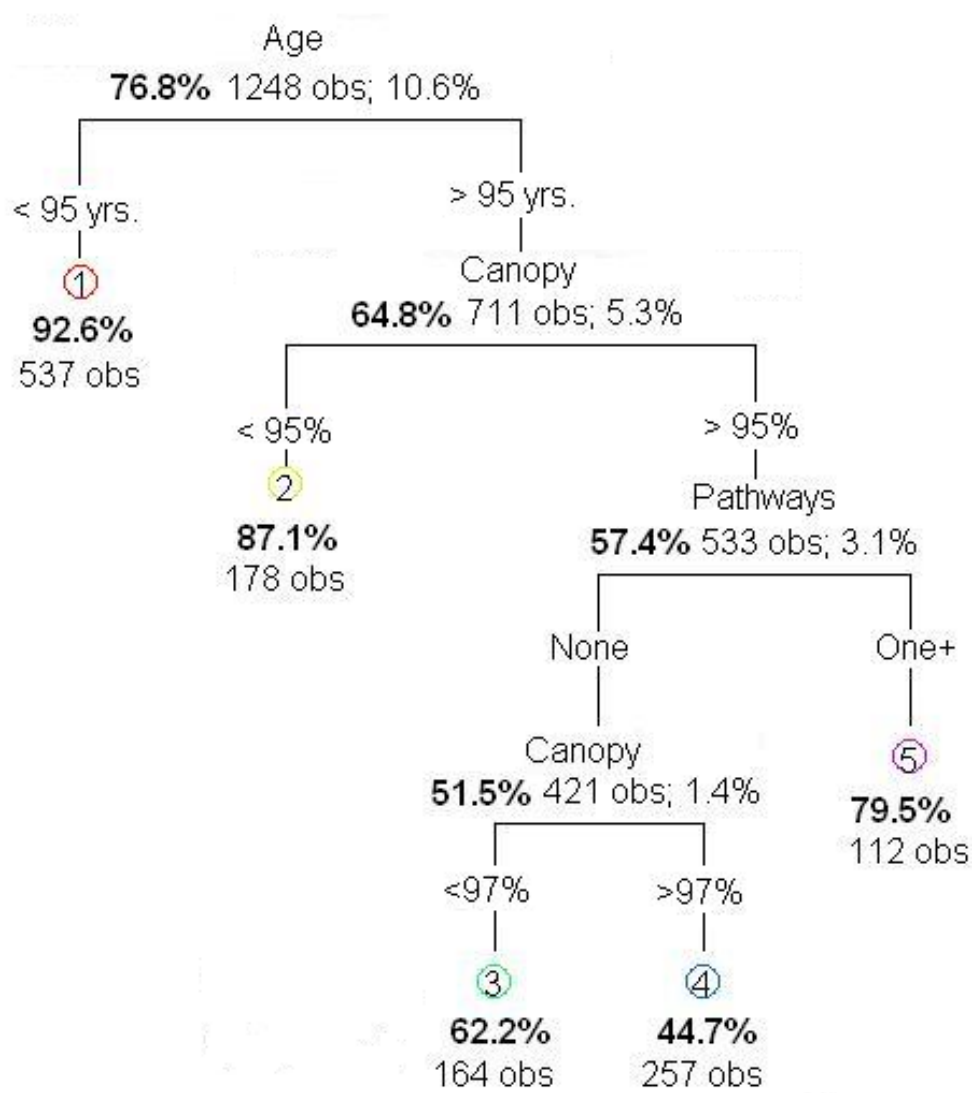


Figure 21

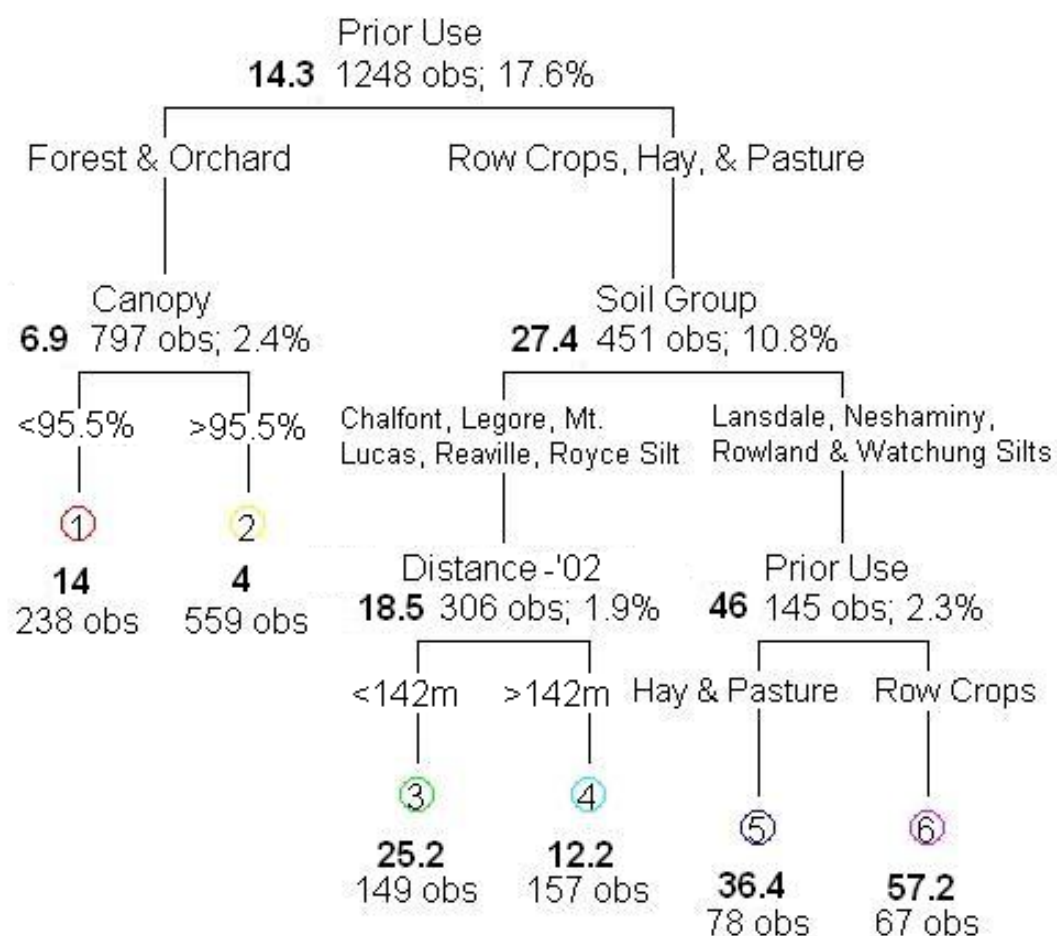


Figure 22

CHAPTER 3

The role of seed dispersal opportunities in the invasive spread of *Microstegium vimineum*.

Abstract: As an annual plant, *Microstegium vimineum* is dependent on successful dispersal of viable seeds to expand its invasive range from year to year. The species can thrive in minimally disturbed sites, but as in its native range, it still tends to be found in the greatest density along disturbed corridors, such as waterways and roads. I surveyed linear transects along intermittent streams and foot trails through eight upland forests of different ages, as well as control transects along neither type of corridor. I determined that *M. vimineum* distribution is strongly, but not exclusively, tied to linear dispersal corridors. Specifically, streams and trails are significantly more invaded than control transects, and *M. vimineum* is distributed much more patchily away from corridors. Transects in young forests were significantly more invaded than those in old stands. Isolated individual patches (along neither streams nor trails) of *M. vimineum* were also observed to expand at approximately 1m per year, although approximately 11% of germinated seeds dispersed farther than 2m from their original patch. This long-distance dispersal was heavily directed by gravity, as such germinants appeared downslope of the parent patch two to four times more frequently than upslope. Management to control this species will be most effective by focusing on exclusion along corridors that could allow entry, particularly in older forests.

Introduction

Although many factors contribute to the invasiveness of a species, propagule dispersal has immediate application to efforts to contain further spread, since the difference between successful and unsuccessful introductions in many cases appears to be propagule pressure (Moody and Mack 1988; Lockwood, Cassey et al. 2005). Despite its importance, this issue is rarely explored for those species that lack obvious dispersal mechanisms. One such invader is the annual grass *Microstegium vimineum* (Trin.) A. Camus (hereafter *M. vimineum* or stiltgrass), which has spread rapidly on the east coast of North America despite its non-specific dispersal syndrome. Although the species is often first noticed in an area along potential dispersal corridors such as roads and streams (Scholz and Byfield 2000; Gibson, Spyreas et al. 2002; Peskin 2005), its movements into other parts of a habitat are much less well understood. This study attempts to define the relevant spatial scales for dispersal in this species, and to understand differences in dispersal mode across those scales.

A number of studies in recent years have highlighted the importance of dispersal processes in invasion ecology. Working with theoretical modeling, Kot *et al.* (1996) demonstrated that invasions can proceed much faster than simple diffusion models would expect if there are even a few long-distance dispersing propagules. Similarly, Moody and Mack (1988) argued that small satellite populations are more responsible for invasion rates than larger established populations. Understanding potential long-distance dispersal corridors and points of entry into a landscape are thus of crucial importance for

controlling and managing problematic invasions. For plant species with obvious dispersal syndromes (by frugivorous birds, for instance)(Deckers, Verheyen et al. 2005; Spiegel and Nathan 2007), understanding movement into a landscape is reasonably tractable, but for those many species which lack such obvious syndromes, prediction can be more problematic. Species whose seeds simply fall from the parent are unlikely to disperse very far or very rapidly, unless they are subsequently carried away by another force (Schupp and Fuentes 1995). For many invasive species, water and animal (including human) movement has been shown to be such a kind of dispersal vector, greatly increasing the success of invasions (Lawes and Grice 2007; Von der Lippe and Kowarik 2007; Will, Maussner et al. 2007).

Community age and structure are additional factors that have been shown to be very influential on plant invasions, and are also often correlated to the presence and type of dispersal pathways (Spyreas and Matthews 2006). Older forests, for instance, often have fewer active roads running through them than younger ones, and to be further upstream in river networks (Aragon and Morales 2003; Pauchard and Alaback 2004). Both of these factors may decrease the propagule pressure from these vectors in older forests. Instead, the slower expansion of individual patches establishing near the edge may be the primary invasion process in these forests [but see(Higgins, Nathan et al. 2003)]. In addition, the structure of older communities is thought to impart resistance to invasion by providing fewer unoccupied niches (Alpert, Bone et al. 2000; Kolb and Diekmann 2004; Parks 2005), and it remains to be seen how such biotic resistance relates to the efficacy of major dispersal pathways at promoting invasion.

Many studies to date on dispersal ecology in invasion have focused on perennial species, which have both sexual and asexual methods of propagation. As such, seeds can start new satellite populations after dispersal, while cloned shoots can expand the boundaries of existing infestations. In the northeastern United States, Japanese barberry (Ehrenfeld 1997) and multiflora rose (Hunter and Mattice 2002) are two widespread shrubs that successfully use both approaches. For an annual plant, however, any range expansion must be driven by widespread dispersal of viable seed, since a lack of clonal growth potential would otherwise limit individual patches to their original extent. In fact, there are a number of examples of prominent invasive annuals that have relied on small seed size, prolific fecundity, and flexible dispersal corridor use to cover wide geographic areas. Some of the more notorious species include cheatgrass (*Bromus tectorum*) in the Mountain West (Knapp 1996) and mile-a-minute vine (*Persicaria perfoliata*) in the Southeast and Mid-Atlantic (Kumar and DiTommaso 2005).

M. vimineum was first recorded as naturalized in Knoxville, TN in 1919 (Fairbrothers and Gray 1972), and thus is a fairly recent invader of concern along the eastern seaboard of the U.S. Over the last 30 years, in particular, the species has become dominant in the herbaceous layer of many hardwood forests in the region, initially in more disturbed stands, but increasingly in less disturbed ones (Redman 1995; Cole and Weltzin 2004). Along with directly competing with native forest herbs and seedlings of woody species for light and other resources (Barden 1987; Oswalt, Oswalt et al. 2007), *M. vimineum* seems to act in conjunction with other invasive species, namely *Berberis thunbergii*, *Rosa multiflora* and exotic earthworms to alter the soil biology of such forests

significantly (Kourtev, Ehrenfeld et al. 1998). Thus, it poses a substantial threat to biodiversity conservation in the forests of the region.

In its native range of eastern and southeastern Asia, *M. vimineum* is typically found in a range of disturbed habitats, particularly riparian systems (Chen and Phillips 2002). Each plant can produce hundreds of seeds if conditions are favorable, and seeds remain viable in the seed bank for up to five years (Gibson, Spyreas et al. 2002). In its native range, it appears typical of many ruderal annual species, relying on a network of ephemeral-available habitat patches to maintain its population. In its invaded range, however, it establishes stable populations in many situations, particularly where light and resource availability remains high. The seeds are very light and likely quite buoyant, and dispersal in mud attached to boots, hooves, and tires is also highly plausible (unpublished observations). When the species was recently documented for the first time in Turkey, it was no coincidence that it was found within riparian corridors (Scholz and Byfield 2000). In its invaded range in North America, *M. vimineum* can be found in a wide range of habitats, but the densest infestations are typically along riparian corridors and roadways (Barden 1987; Redman 1995; Luken and Spath 2002; Cole and Weltzin 2004). The connection to roads is particularly apparent along the fronts of the species' expanding range. In the northern Appalachians, for instance, Peskin (2005) found the species almost exclusively around culverts passing underneath logging roads in otherwise uninvaded forests.

In order to document the importance of adequate dispersal corridors for the spread of *M. vimineum*, I used observational studies at several spatial scales to determine which

types of corridors tended to be most invaded, as well as what the pattern of invasion was along each corridor. By comparing this pattern to that in habitat without such corridors, I hoped to better explain the role of corridors in invasion. In addition, isolated upland patches were observed to determine realized rates of patch expansion in a year. The studies were designed to test the following hypotheses:

1) *M. vimineum* disperses preferentially along waterways, roads, and trails, with streams developing more homogenous and denser invasions than roadways, which in turn will be more invaded than general upland habitat.

2) Isolated patches of *M. vimineum*, unconnected to obvious dispersal corridors, will expand only slowly, while those on sloping sites or with other possible dispersal opportunities will have more long-distance dispersal from year to year.

Methods

Study Area

These studies were conducted at sites in the Sourland Mountains of west-central New Jersey (approximate coordinates: 40°28'N 74°42'W). The Mountains are a set of low hills covering an area of approximately 250 km², which are underlain by diabase bedrock that projects between 50 and 100m above the surrounding sedimentary substrates of the Piedmont. Since European settlement in the late 1600s, the area was used by small subsistence-level farmers, raising and gathering a variety of wild and domestic products, and as lumbered woodlots of wealthier lowland farms (Luce 2001). Today the region is

dominated by forests of many different ages and land use histories. This study took place in both old (> 80 yrs. continuous cover) and young stands (<75 yrs.), as determined by examinations of aerial photographs, the earliest of which were taken circa 1935. Stands of various ages were chosen for this survey in order to determine if observed differences in invasion intensity between younger and older stands (see chapters 1 and 2) were reflected in differences of invasion along dispersal corridors. Dominant tree species in the region include oaks (*Quercus alba*, *Q. rubra*, *Q. velutina*), hickories (*Carya ovata*, *C. cordiformis*, *C. tomentosa*) and maples (*Acer saccharum*, *A. rubrum*), as well as *Liriodendron tulipifera*, *Betula lenta*, *Fraxinus americana*, *Fagus grandifolia*, and *Tilia americana*. Dominant shrubs in the area include both native species (*Lindera benzoin*, *Hamamelis virginiana*, *Vaccinium corymbosum*) and non-native invasive species (*Berberis thunbergii*, *Rosa multiflora*, *Rubus phoenicolasius*). Generally, young forests were on more level terrain and had canopies of *A. rubrum* and *L. tulipifera*, while old forests were on steeper topography with a more mixed hardwood canopy. Soils are either based on igneous bedrock (diabase) or semi-metamorphic shales (argillite), but in either case they have low water-storing capacities except where clay fragipans hold water near the surface, which is a very common occurrence. As a result, the region has an extensive network of vernal pools and streams that slowly dry up over the course of the summer, but nonetheless act to link much of the region in terms of surficial hydrology (Mulhall 2004).

Observations for these studies took place primarily at a 1200-ha county park at the northern end of the range, as well as at two smaller and adjacent forest preserves in the center of the mountains.

Observation Procedures

To test hypothesis 1 (preferential dispersal along corridors), during the winter of 2006 I walked a series of 100m linear transects along a stream/seasonal rivulet, trail/two-track, or through upland habitat that had neither of these features (control). Three transects, one of each type, were placed in areas of forest with an approximate diameter of 250m. Stream and trail transects were located on representative stretches of their linear feature, while control transects ran haphazardly across the terrain as a series of five 20-m segments, with a turn between 0° and 90° after each segment. For each transect, the linear extent of every *M. vimineum* patch encountered was recorded, as well as the uninvaded distance between patches, if any. The number of invaded patches along the transect was also recorded. Finally, the local intensity of invasion measured the distance from the transect line over which *M. vimineum* was observed (Fig. 23). Each patch was assigned one of four *M. vimineum* cover classes: extending <1m outward from transect, <2m, <3m, or >3m. By assigning an ordinal ranking of 1-4 for these cover classes, an intensity metric was calculated for each patch ("patch width") as well as for each transect ("invasion intensity"). Invasion intensity was derived by multiplying the proportional lengths of patches running through each class, and summing across the entire transect. Thus, intensities could range from 0 (no invasion) to 4 (entire length running through a patch extending >3m from the transect). Three transects of each type (stream, trail, or control) were surveyed in four young and four old forest stands, for a total of 72

transects. Within each stand stream transects were chosen from unique waterways, but trail transects were part of interconnected trail networks.

To test hypothesis 2 (expansion of isolated patches), nine isolated (no other *M. vimineum* closer than 15m) patches of various sizes (0.5m^2 to 8m^2) were identified in the fall of 2005 and six more (size range: 1m^2 to 40m^2) in the fall of 2006. In 2005, two transects, extending from opposite sides of the patch, were marked out from each patch. Depending on plot location on the slope, transects were chosen to run out either laterally (along the contour) or uphill and downhill, resulting in 5 lateral, 6 uphill and 7 downhill transects being surveyed. These transects were then resurveyed in the spring of 2006. New plants appearing within 20cm of the transect were recorded, to a limit of 8m from the prior year's patch boundary (Fig. 24). For the 2006 set, all new plants emerging around the original perimeter were measured, with both a distance and bearing category (N-NE, NE-E, etc.) from the old boundary recorded. For each patch, the uphill bearing was measured, and the bearing categories on either side of that azimuth were designated as 'uphill', the adjacent two were designated 'uphill-lateral', the following two 'downhill-lateral' and the two opposite the original bearing were 'downhill.' In both years, conditions around the patch that might influence dispersal, such as deer trails or eroded gullies indicating water flow, were also noted. This study had no mechanism to distinguish between newly-dispersed seeds and seeds present in the seed bank from previous years, however. Thus it is actually measuring realized expansion of patches rather than actual dispersal rates. All patches were located in the Somerset County Park, Hillsborough, NJ.

Statistical analyses were carried out using SAS Version 9.1. Differences in presence and intensity along corridors were analyzed using two-way ANOVAs (PROC GLM) with age and pathway type as independent variables. Tukey's HSD test was used for pairwise comparisons. Differences in patch expansion distances and direction were analyzed using PROC MEANS, PROC GLM, and PROC UNIVARIATE. Distances were $\log_{10}$ -transformed before entering them into linear models to restore normality. Dispersal distances for each year were compared to an exponential distribution probability density function where $\lambda = 25/\text{mean distance}_{\text{year}}$. The null model was then calculated as $\text{probability}(\text{distance}, x) = \lambda e^{-\lambda x}$. A χ^2 test was then applied for each 25cm distance category to compare the statistical similarity of observed to expected probabilities.

Results

Corridor Dispersal

The occurrence and extent of *M. vimineum* invasion was heavily influenced by the age of the forest through which the transect passed, and to a lesser extent by the type of dispersal corridor the transect followed. For all five metrics of invasion examined, a two-way ANOVA involving both age and type is highly significant ($p < 0.0001$), although age is generally more influential than corridor type (Table 10). In terms of overall invasion percentage and intensity, transects in young forests are much more invaded than in older forests (Fig. 25). Younger transects are twice as invaded as older transects by percentage, and four times more invaded by a measure of intensity. Corridor type,

however, only made a difference in terms of the percent invaded, as control transects were less invaded than those along either streams or trails. Invasion intensity, though, is statistically equivalent among the corridor types.

The size and number of individual patches was also strongly influenced by forest age, although corridor type did not have as marked an effect. Old and young transects had a similar number of patches, on average, but patches along old transects were smaller and more widely spaced (Fig. 26). In contrast, corridor type had no effect on patch size and spacing, but control transects did have significantly more patches than stream transects, with trail transects being statistically equivalent to both. Only one metric was affected by a significant age * type interaction. Specifically, old transects had similar numbers of patches no matter what corridor they were surveyed along, but young transects along streams had fewer patches than along trails, which in turn had many fewer patches than control transects. In other words, many young transects along streams passed through large stands of *M. vimineum* which covered all or nearly all of the transect, while control transects passed across smaller and more numerous patches.

Patch Expansion

-- Distance --

Realized dispersal of *M. vimineum* seeds from parent patches extended, on average, less than 1m per year in the absence of dispersal corridors such as roads, trails, and streams (Fig. 27). However, individual long-distance germinants were recorded at up

to 8m and 2m from the parent patch in 2006 and 2007, respectively, and distributions for both years are clearly right-skewed. Comparing the dispersal distances of each year to an exponential probability curve reveals some significant differences from expected. In 2006, particularly, actual germinants within one meter of the original patch are more numerous than expected, after which they tend to be less numerous than expected. At approximately 5m from the parent patch, however, there are significantly more germinants than expected again, and this long-distance surplus continues through to the farthest distance measured at $\approx 8\text{m}$. In contrast, germinants in 2007 are significantly more numerous than expected up to 1.5m from the periphery, and beyond that distance conform to expectations. One explanation for the difference between years may lie in the local weather patterns over those years. Records from the Wertsville, NJ station ($40^{\circ}27'\text{N}$ $74^{\circ}48'\text{W}$) reveal that although late summer was warmer and drier during 2005 (the growing season before surveying) than in 2006, October of 2005 had rainfall 25cm above the mean, and 16.5cm higher than the same month in 2006. The large storms seen during October '05 may have produced abundant overland water flow, which would have coincided with seed maturation and shatter, and potentially dispersed some seeds much further than expected.

-- *Direction* --

The direction of patch spread appears to be determined mostly by gravity and topography, although any of the linear dispersal corridors mentioned earlier often superseded gravity-based directionality if present. In both surveyed years, new plants emerged downhill from original patches 1.5-3x more frequently than uphill, with lateral

(along-slope) distributions falling intermediate to those (Figure 28). Median dispersal distances, however, were more variable between years (Table 11), with more long-distance dispersal in 2006. In both years downhill germinants were farther than plants on the other bearings from the original boundaries. Strikingly, maximum dispersal distances were similar in all directions, although seeds traveled slightly farther downhill in both years. Smaller (and presumably younger) *M. vimineum* patches were also considerably more productive in terms of boundary-expanding plants on an area basis than larger patches (2-sample t-test $t_5 = 6.36$, $p = 0.0014$). Patches less than 5m^2 in size generated 254.6 plants/m^2 on average outside of their original borders (s.e.=4.8), while patches larger than 10m^2 created only 82.9 m^{-2} (± 14.4 ; Fig. 29).

Discussion

Taken together, these studies illustrate the rapid population expansion that is possible for *Microstegium vimineum* when sufficient dispersal opportunities are present. The corridor transect study underlines the importance of streams and trails as *M. vimineum* first percolates into landscapes (Christen 2005; Peskin 2005). As invasion proceeds, the role of these pathways diminishes, as seen in the different patterns of invasion between young and old forests. Nevertheless, the high overall percentage of invasion, even for transects removed from obvious pathways and in older forests, illustrates the extent to which this species has become widespread in many eastern forests. The densest and most extensive patches of *M. vimineum* are found along waterways, as high water during seasonal flooding can disperse seeds very widely from a

central corridor (Gibson, Spyreas et al. 2002). Trails support statistically similar populations, though, and at least for small seasonal streamlets it seems their primary benefit to stiltgrass is as a dispersal pathway rather than being an edaphically richer microhabitat. Without dispersal corridors, invasion of this species is likely to occur only slowly, as shown in the patch study. As with many other herbaceous species not specialized for dispersal, though, the abundance and light weight of these seeds increases the probability that transport via mammals (either in ecto- or endozoochory) can establish patches in areas distant from primary dispersal corridors (Pakeman, Digneffe et al. 2002). The results of this more stochastic, short distance seed dispersal are seen in the greater patchiness of transects through uplands and in older forests.

In addition to providing corridors for seed dispersal, trails/roads and streams are also disturbed habitats, and as such may present better areas for establishment and growth. Although dispersal distance largely constrains the rate of expansion (Cain, Milligan et al. 2000; Nehrbass, Winkler et al. 2007), many propagules benefit from disturbance to establish no matter how far they've dispersed (Etienne, Wertheim et al. 2002; MacDougall and Turkington 2005). Particularly for annual plants, which are often small-seeded and lacking large reserves for establishment, the link between disturbance and dispersal is a crucial one. Removal of competing vegetation or organic matter by traffic and water can enhance germination (Kellogg and Bridgham 2004; Gabbard and Fowler 2007). In forested communities, dispersal corridors are often closely correlated with canopy gaps, where higher light levels can allow many exotic species to establish (Parendes and Jones 2000). Corridors in the surveyed sites are too narrow to create

significant canopy gaps, but small-scale disturbance of the litter layer may be greatly enhancing stiltgrass establishment.

The strong difference in *M. vimineum* invasion between older and younger forests reinforces findings from other research (see Chapters 1 and 2), and likely comes from two sources. First, older stands in this region have more developed shrub layers than in younger stands, and the additional shade they create leads to smaller areas with suitable light levels for *M. vimineum* (Cole and Weltzin 2005). Thus, even when stiltgrass seeds arrive in older forests, they often do not establish extensive stands, as seen in an average invasion density along the sampled transects one-quarter that of younger stands. In other words, while both phalanx- and guerilla-type expansion (Ye 2006) are possible in younger stands, the increased understory competition in older forests often restricts phalanx expansion. Second, due to their landscape position on rougher, less accessible terrain, older stands have experienced less *M. vimineum* propagule pressure. This is true for a large variety of invasive plants in recently afforested regions (Lundgren, Small et al. 2004; Parks 2005; Von Holle and Motzkin 2007). As *M. vimineum* was being introduced to the landscape in the mid-20th century, forests regenerating on marginal agricultural lands, mostly closer to human activities and settlements, absorbed the bulk of the new seeds, potentially buffering older stands from the invasion front for some time (Foster 1992; Redman 1995). Deer movement, likely a major vector for upland seed dispersal (Pakeman, Digneffe et al. 2002; Henrik-Bruun and Poschlod 2006), also tends to be lower in interior forest cores than the edge habitat of young forests (Adams 2003). As a result, older stands receive most of their invasives along linear invasion corridors

carrying seed from younger stands or grasslands on their border, and to have limited invasion patches in most of their area.

Several trends from the studies of individual patch expansion stand out. First, for many patches, realized rates of spread are moderately slow (10-50 cm/yr) and limited to seeds falling directly from parent plants at the edge of patches. In both 2006 and 2007 the vast majority of the plants germinated only this far from the parent patch, even though the late season rainfall totals in each year differed significantly (2006 was a drier growing season than 2007 in the Sourlands). *M. vimineum* would not have become such a prominent invader so quickly over the last 30-40 years moving at these rates of expansion, so much of the expansion is likely due to less frequent, but longer-distance ($>1 \text{ m yr}^{-1}$) dispersal events (Moody and Mack 1988; Kot, Lewis et al. 1996). It was clear that slope position can play an important part in this dispersal, with areas downslope of patches receiving more seeds than upslope areas in both years. The simple effect of gravity, as well as surface run-off during winter and spring rain events, is likely the main reason for this bias. Very long-distance dispersing seeds appeared in all directions from a patch, though, and point to the probability of eventual patch expansion, even upslope. In addition, patches with some sign of mammal or water movement through them tended to show longer potential dispersal distances, even against slope gradients (Kellogg and Bridgham 2004). This may in part be due to the leaf litter disturbance allowing plants in the existing seed bank to germinate, rather than representing new dispersal. Repeated observations at these patches, each of which was only measured for one season in these studies, would be very helpful for more precisely determining rates of expansion and

differentiating potential versus realized dispersal. Repeated measurements would also aid in quantifying the role of interannual climatic variation in shaping invasion patterns.

In summary, data from these studies clarifies the dramatic importance of dispersal corridors such as trails and waterways for the rapid spread of *M. vimineum* in hardwood forests of the Mid-Atlantic states. The lightweight and abundant seeds of the species have allowed it to exploit such corridors in invading large expanses of many forests, particularly younger stands with more disturbed plant communities and soils. Smaller-scale dispersal is gradually introducing the species to portions of forests far from such obvious corridors, where the limitations provided by biotic interactions are likely to constrain the ultimate distribution of *M. vimineum*.

Table 10. Summary of two-way ANOVA results for transects through two forest ages (Young and Old) and three corridor types (Stream, Trail and None). Significant differences between ages and types are shown under the relevant results, and were tested using Tukey's honestly significant difference, with $\alpha = 0.05$.

	% Invaded	Invasion Intensity	# of Patches	Mean Patch Width (m)	Mean Gap b/w Patches (m)
Age	***	***	ns	***	***
	Y>O	Y>O		Y>O	O>Y
Type	**	ns	*	ns	ns
	S=T>N		N>S		
Age*Type	ns	ns	**	ns	ns

Significance codes: *** = $p < 0.0001$, ** = $p < 0.001$, * = $p < 0.05$, ns = not significant at $\alpha = 0.05$

Table 11. Dispersal distances and direction of *M. vimineum* from parent patches in two sample years. Patches in 2006 were sampled in only two transects running out from the parent, while 2007 measurements include germinants in all directions. Statistics in the “Median Distance” column are GLM results comparing log-transformed means of dispersal distances in three directions from the parent patch for each year. Means with different letters in a given year are significantly different at $\alpha=0.05$ under a Tukey’s honestly significant difference test.

	# of Plants	% of Plants in a Given Year	Max. Distance (cm)	Median Distance (cm)
2006	(per transect)			$F_{2,1191}=13.3, p<.0001$
Downhill	86.9	65.6	814	39.0 ^A
Lateral	59.0	9.9	611	24.5 ^C
Uphill	41.7	24.5	688	34.0 ^B
2007	(for all patches)			$F_{3,6695}=14.8, p<.0001$
Downhill	2596	38.8	212	23.0 ^X
Down-Lateral	1758	26.2	192	18.5 ^Y
Lateral-Up	1091	16.3	158	
Uphill	1251	18.7	203	17.0 ^Y

Fig. 23. An example of the transect methodology in this study. Total length of each transect was 100m, and the percentage invaded was found by summing the length passing through each stiltgrass patch (solid dark lines across gray patches) on the transect. The number of patches across the transect was also counted, and intensity was determined from the average width of each patch (dotted lines perpendicular to transect).

Fig. 24. Survey design for detecting germinants around stiltgrass patches. In 2006, only germinants within 20cm from two transects were recorded, while all germinants around the perimeter were recorded in 2007.

Fig. 25. Analysis of *M. vimineum* invasion patterns along transects through three corridor types (stream, trail, upland; light bars) and two forest ages (young and old; dark bars). Standard errors shown. (A) percent of each 100m transect invaded, (B) the mean invasion intensity per transect (scale of 0-4). Within types and ages, groups with different letter labels are different at $\alpha = 0.05$.

Fig. 26. Analysis of *M. vimineum* invasion patterns along transects through three corridor types (stream, trail, upland; light bars) and two forest ages (young and old; dark bars). Standard errors shown. (A) mean number of patches per transect, (B) mean width of patches, and (C) mean distance between patches. Within types and ages, groups with different letter labels are different at $\alpha = 0.05$.

Fig. 27. Histogram detailing distances new plants appeared from original boundaries of different *M. vimineum* patches in two sampling years.

Fig. 28. Percentage of new germinants appearing in several topographic directions from parent patches in two consecutive sampling years, pooled across nine patches in 2006 (a) and six different patches in 2007 (b). There is an additional direction category in 2007 because sampling protocols were changed between years. The length of each vector is proportional to the median distance germinants traveled along that path.

Fig. 29. Relationship of patch area to relative productivity of germinants. The six patches were sampled in 2007.

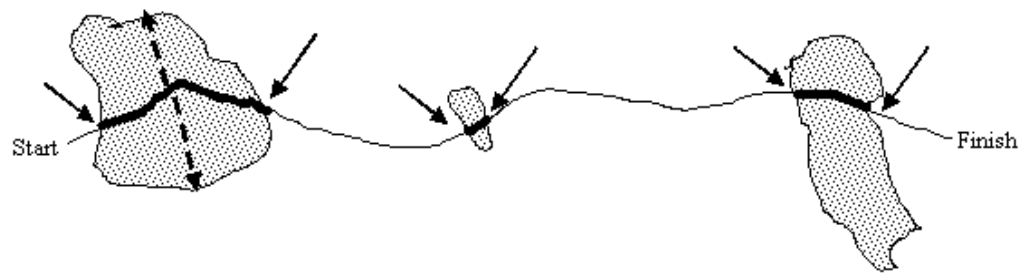


Figure 23

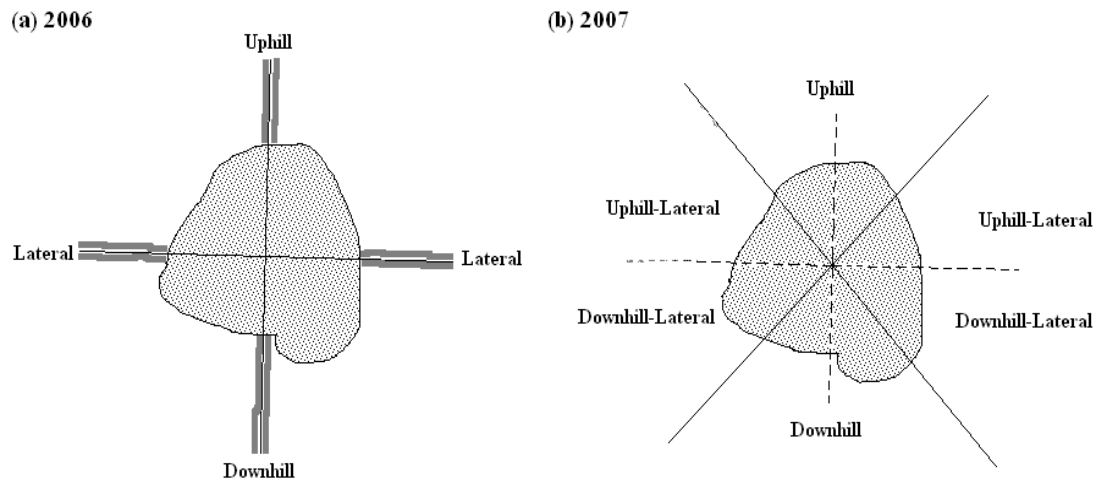
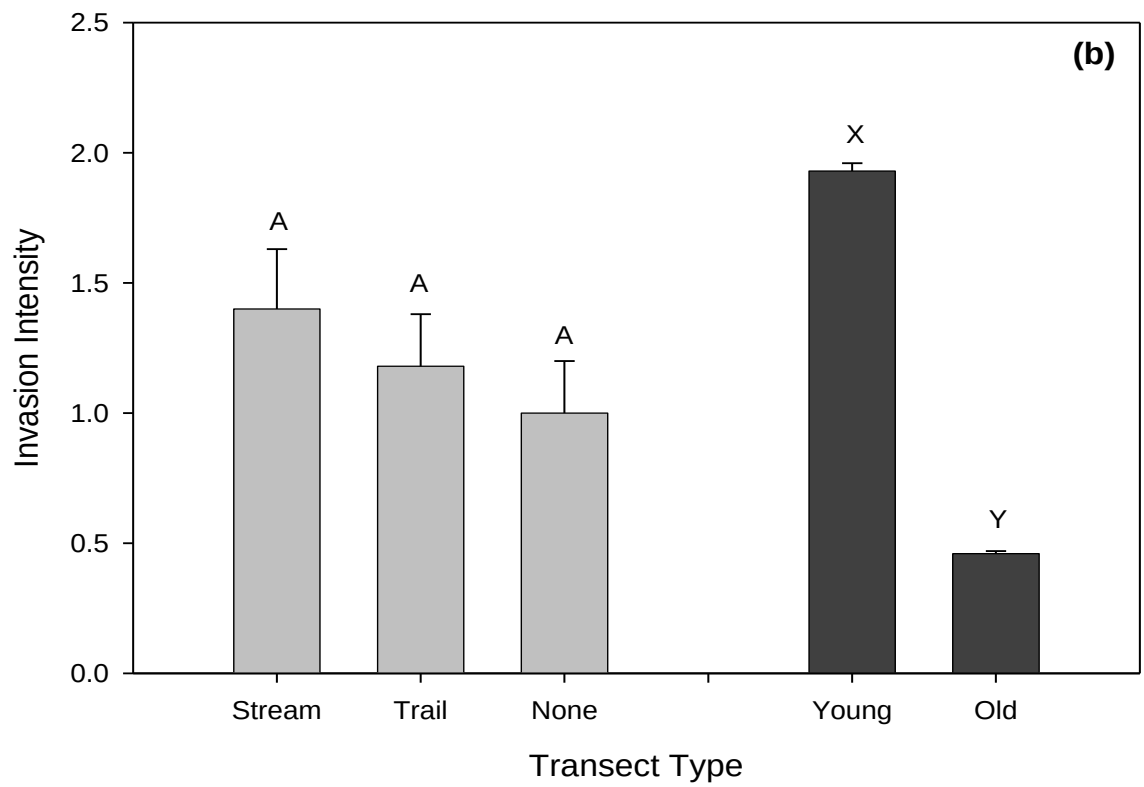
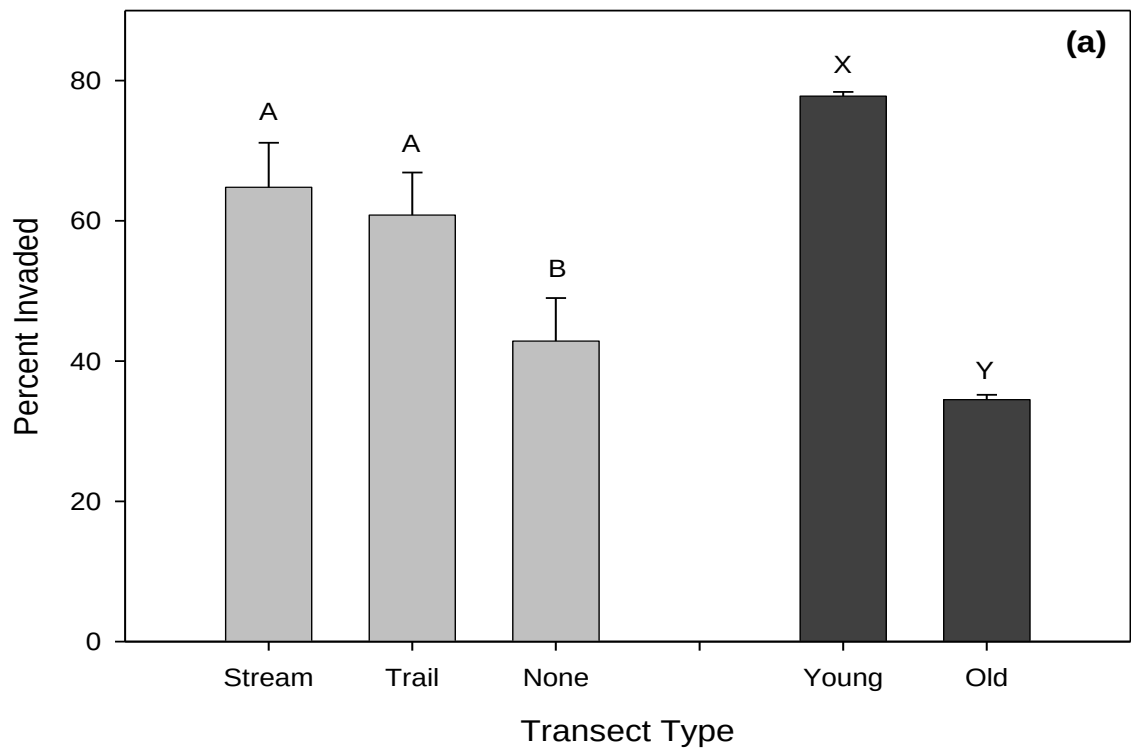


Figure 24

**Figure 25**

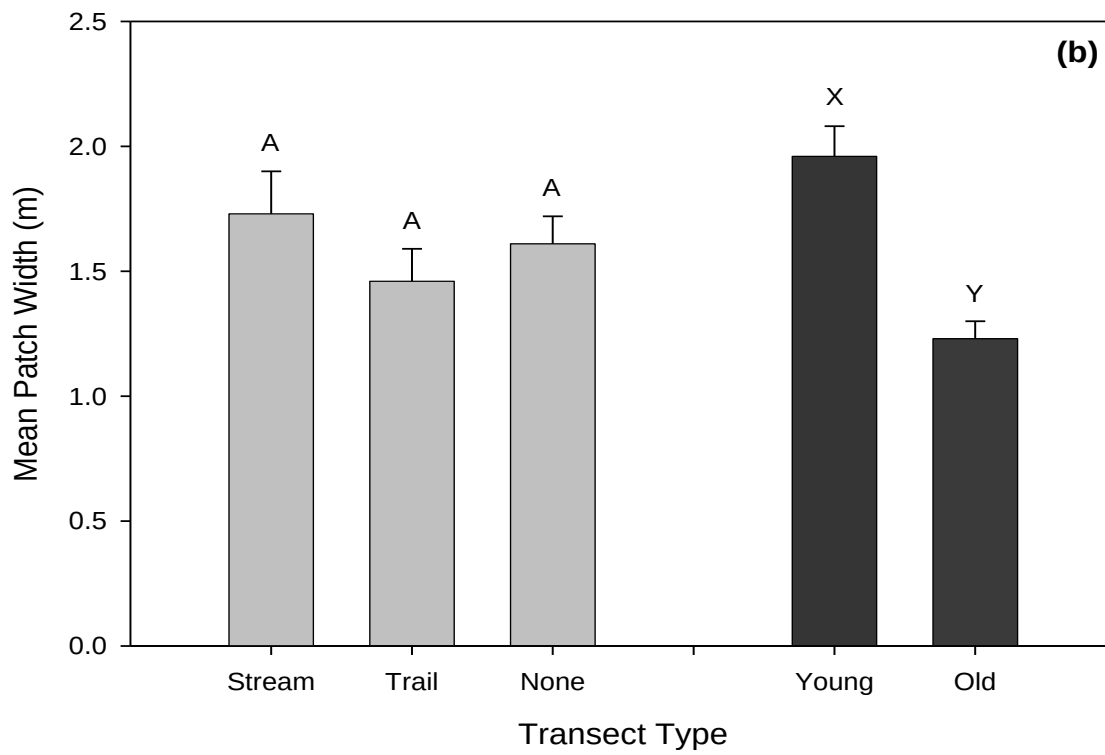
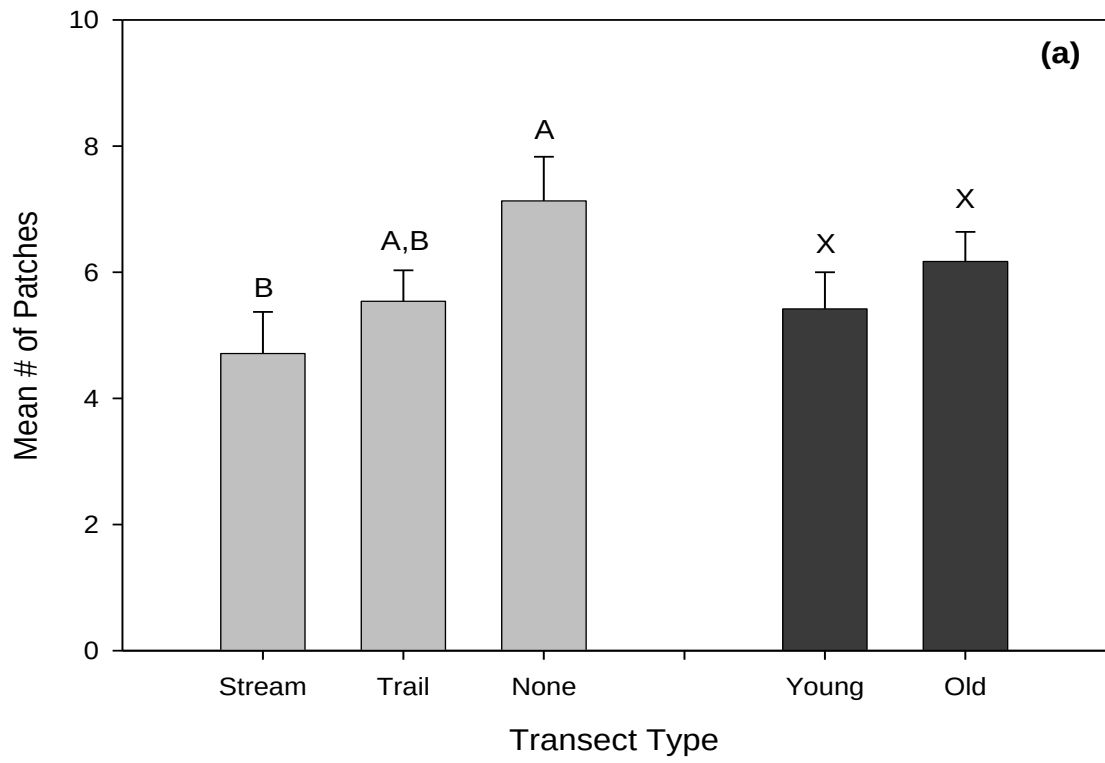


Figure 26a and 26b

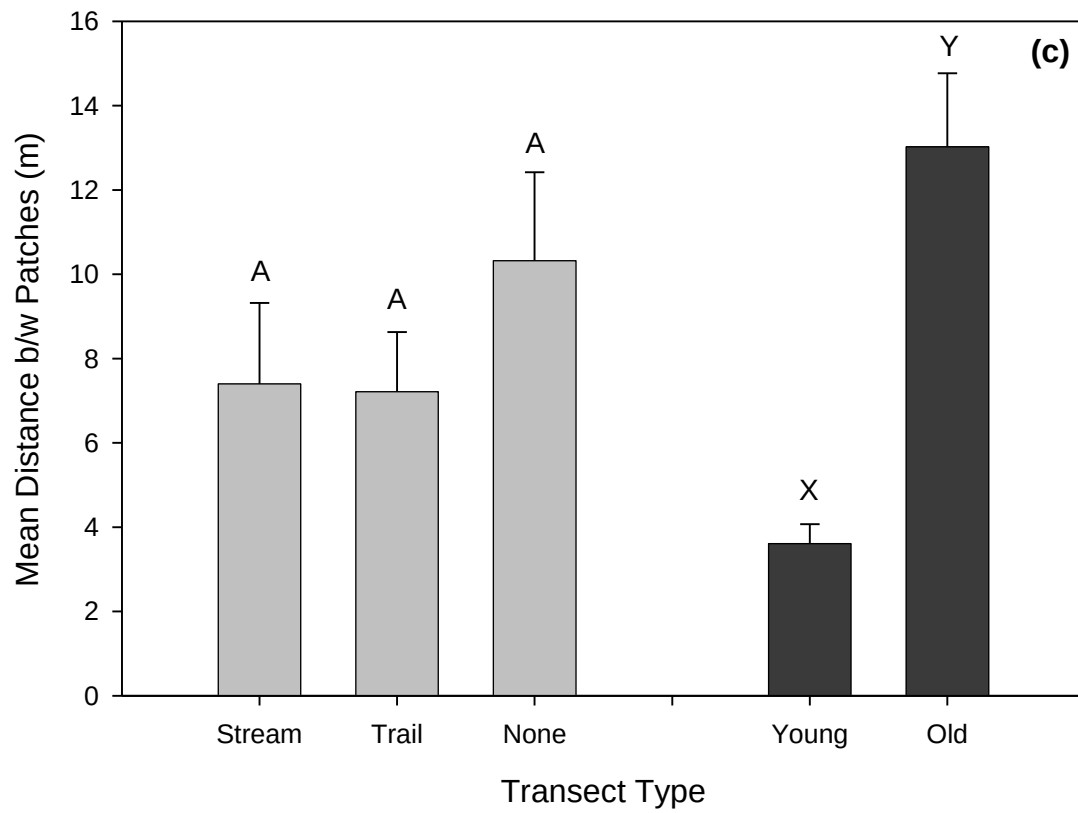


Figure 26c

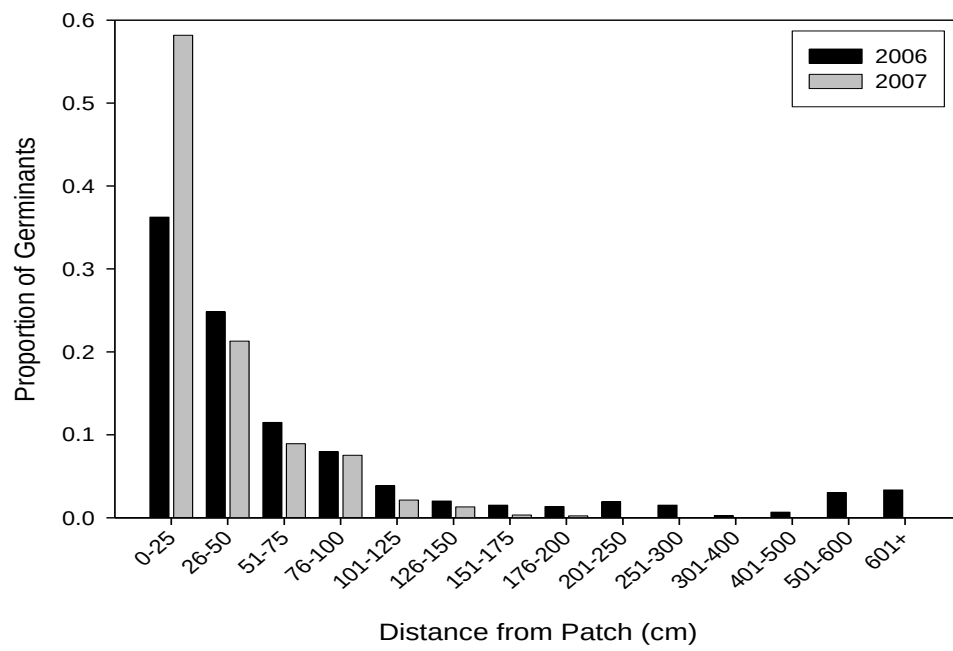
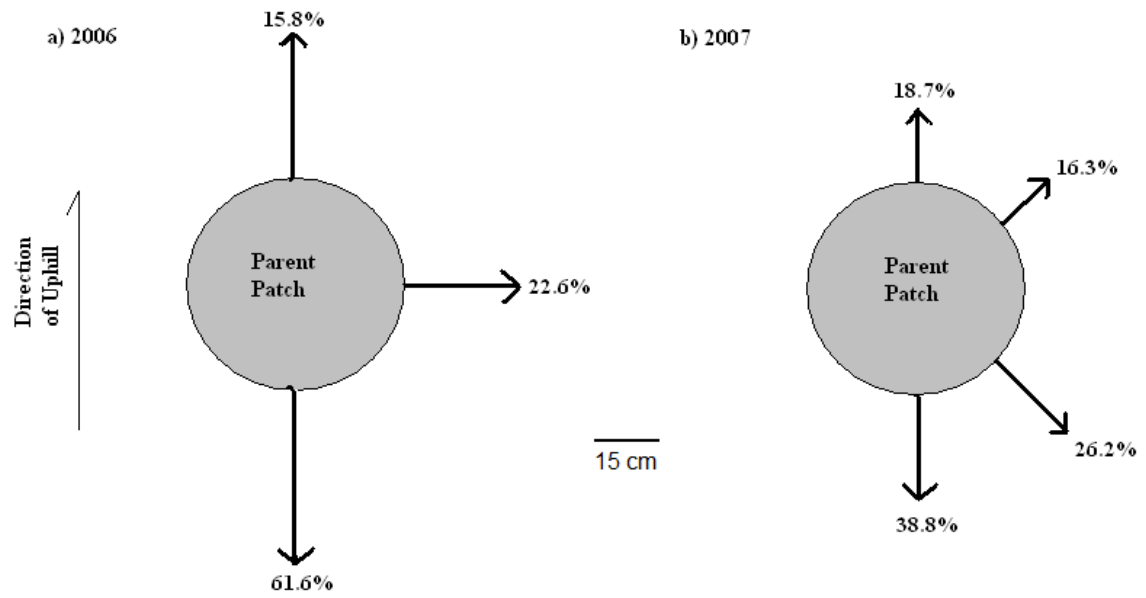
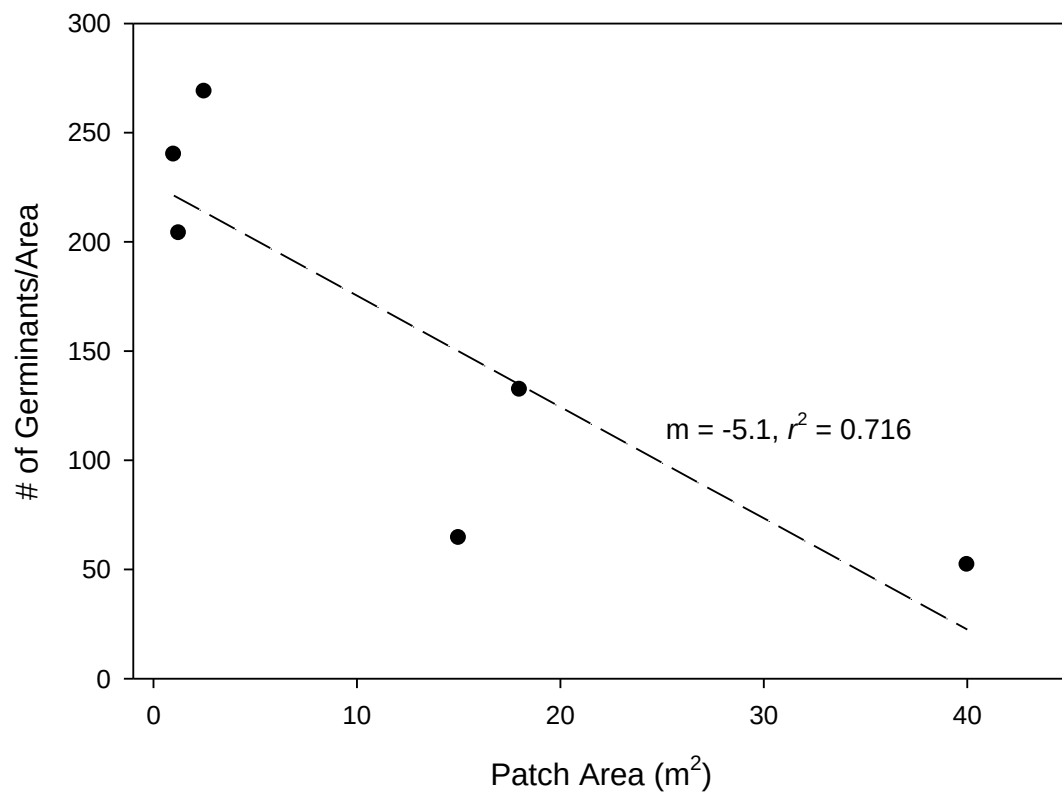


Figure 27

**Figure 28**

**Figure 29**

CHAPTER 4

Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*.

Abstract: The issue of heterogeneity in the distribution of invasive species remains an important area of research, not least so that a better distinction between fixed-size and expanding populations can be made. Although increasingly widespread in the eastern U.S., the invasive grass *Microstegium vimineum* has apparent habitat limitations in field settings, especially forests with mature canopies and litter layers. In order to tease apart these related constraints, seeds of *M. vimineum* were sown under differing levels of shade (w/ and w/o shrub canopies) and leaf litter depth/disturbance in mature forests in central New Jersey. Populations were monitored for germination and survival rates, as well as growth and fecundity of surviving plants. Seed plots exhibited germination rates from 20-40%, with rates not significantly different among different levels of shade and depths of leaf litter. Seeds sown on top of undisturbed litter, however, had much higher mortality in the earliest stages of the growing season. As the season continued, survival dropped, particularly in plantings shaded by shrubs. Many of the germinants did not survive long in any of the treatments, with the heaviest die-offs within three weeks of germination. By the end of the four month growing season, only 7.5% of the original germinants had survived to flowering stage. On average, surviving plants had an above-ground biomass of 16.4 mg and produced 6 spikelets. With very high deer densities and subsequently reduced shrub cover in many of the states where this species is expanding, it is likely to continue its population increases without active intervention.

Introduction

Although a great deal of progress has been made over the last several decades in our understanding of plant invasions, many questions still remain. One of these basic questions simply concerns the determinants of heterogeneity in an invasive plant species' distribution, both across a landscape and within a habitat (Sakai, Allendorf et al. 2001; Rouget and Richardson 2003; Hill, Tung et al. 2005). Species-specific tolerances for light, water, and nutrients are likely to play a large role in constraining distributions, but the issue becomes much less clear when other substantial changes to ecosystems are taking place contemporaneously (Dukes and Mooney 1999; Bohlen, Groffman et al. 2004; MacDougall and Turkington 2005). Increases in herbivore populations often have dramatic effects on plant communities, and can promote invasive plant species at the expense of their native competitors (Kellogg and Bridgham 2004; Morrison, Lubchansky et al. 2007). Populations of white-tailed deer (*Odocoileus virginiana*) in the eastern United States, for instance, have sharply increased over the last few decades, resulting in overbrowse of many native plants and more opportunities for non-native invasive species to establish (Pedersen and Wallis 2004; Rooney, Wiegmann et al. 2004; Griggs, Rock et al. 2006). One invasive species capitalizing on these alterations is *Microstegium vimineum* (Trin.) A. Camus (Poaceae; hereafter *M. vimineum* or stiltgrass), an annual grass with an often patchy local distribution. Reductions in the shrub density of many forests in the region, often due to deer browse, may be greatly facilitating this species' invasion (Rooney, Wiegmann et al. 2004; Griggs, Rock et al. 2006), both by allowing

more light to reach the forest floor and by reducing the amount and thickness of leaf litter which might otherwise inhibit establishment (Dighton 2000; Oswalt and Oswalt 2007).

A major emphasis in invasion research to date has been the concept of biotic resistance, whereby the composition of a community may largely determine the success of an introduced species (Stohlgren 2006; Fridley 2007). A number of studies have examined species and functional diversity of experimental communities as they relate to invasion success, with mixed results (Stohlgren, Binkley et al. 1999; Levine, Vila et al. 2003; Gilbert and Lechowicz 2005). For many species, however, a simpler measure of biotic resistance may be most pertinent, namely structural integrity of the invaded community (Xu, Ye et al. 2004; Britton-Simmons 2006). When entire structural elements, such as vertical strata in forested systems, are altered or missing, they may create conditions of higher resource availability that promote invasion which would not otherwise have been able to occur in the community (Davis, Grime et al. 2000; Davis, Thompson et al. 2005). In this view, particular species composition may not be as important as insuring that all relevant structural components are present (Pokorny 2005). In the invasion of *M. vimineum*, a form of indirect trophic cascade may be facilitating the species' expansion, where increasing deer populations are diminishing the cover of forest shrub species, thus removing a primary competitor for light (Pedersen and Wallis 2004). At the same time, the loss of shrub layers is changing the dynamics of leaf litter creation and maintenance, by altering inputs and forest floor wind patterns.

M. vimineum is a relatively new (<90 years) and rapidly spreading non-native invasive plant in New England and the northern Appalachians (Fairbrothers and Gray

1972; Hunt and Zaremba 1992). The species is a concern because it has a demonstrated ability to invade the herbaceous layer of intact forests, as well as disturbed sites such as old fields and field margins (Redman 1995; Oswalt, Oswalt et al. 2007). Like many of its competitors, *M. vimineum* depends on efficient use of fleeting sunflecks on the forest floor for its success, and tends towards a sprawling, open habit to accomplish that (Horton and Neufeld 1998). Growth can be sustained at light intensities as low as 4-5% of full sunlight (Gibson, Spyreas et al. 2002), and as an annual, individual plants can invest a large proportion of photosynthates in reproduction (Claridge and Franklin 2002; Cheplick 2005). To maximize this approach, *M. vimineum* also uses the C_4 photosynthetic pathway, which, although common in grassland species, is quite rare in forested situations and allows *M. vimineum* to photosynthesize efficiently even in the drier conditions of late summer (Winter, Schmidtt et al. 1982), as well as to avoid extensive investment in below-ground biomass (Horton and Neufeld 1998). The preponderance of stiltgrass in a wide variety of forested situations suggests that tree canopy shade is rarely enough to fully exclude it, and that intact shrub or understory layers are crucial for shading the species out. Several studies from riparian forests have shown a strong negative correlation between the presence of woody understory species and the density of invading *M. vimineum* (Barden 1987; Cole and Weltzin 2005).

The rapid expansion rate of *M. vimineum* along the eastern seaboard is another surprising aspect of this species' biology. In its native range, the species is a common one in ditches, forest edges and other disturbed habitats (Chen and Phillips 2002). It has expanded well beyond those constraints in North America, however, suggesting that other disturbance-promoting factors are at work throughout the region (Redman 1995).

The most likely covariate is the dramatic increase in deer densities over the last 40-50 years, which has occurred coincidentally with an increase in their preferred habitat after agricultural abandonment. Numerous studies have illustrated the strong link between increasing deer density and decreasing native biodiversity and productivity in forest understories (Pedersen and Wallis 2004; Rooney, Wiegmann et al. 2004; Griggs, Rock et al. 2006). This removal of native competitors has likely contributed to increases in the populations of a variety of invasive species, especially those unpalatable to deer. At the same time, without a robust layer of native shrubs, less leaf litter is being deposited, and that which is shed is more easily carried away from the area either by wind or water moving more freely through the understory. Another factor which is reducing leaf litter thickness in many forests is the presence of non-native earthworms, which break down litter more quickly than native species as a result of their feeding strategies (Bohlen, Groffman et al. 2004; Hale, Frelich et al. 2005). In short, the forest floor of many sites is a much more favorable environment for a disturbance-tolerant species such as *M. vimineum* than it was before recent expansions in herbivore and detritivore populations.

Another enduring issue in biological invasions is clarifying the potentially disparate controls on different demographic stages of an invasive species (Jongejans, Skarpaas et al. 2007; Kota, Landenberger et al. 2007). The transition from seed to seedling, for instance, may depend on a different environmental condition than that from juvenile plant to reproductive adult. Thus, if only one condition is favorable for the invader, it may not be able to expand if controls on the other stages are unfavorable (Davis and Thompson 2000). This is especially true for annual species, which depend on moving from seed to seed within one growing season, and can not spread simply through

vegetative growth. Knowledge of the controls at each transition can greatly improve our management efforts for these species, making them both more efficient and effective.

In the case of *M. vimineum*, it is still uncertain what the relative importance of each demographic transition is for its spread. The species is known to possess a relatively long-lived seedbank (Gibson, Spyreas et al. 2002), which provides it with some interannual resilience, though the majority of seeds germinate within the first two years. When germination occurs, though, thick litter layers may inhibit establishment (Oswalt and Oswalt 2007) by either preventing hypocotyls' access to light (i.e. -litter burying seed) or radicles' contact with soil moisture and nutrients (i.e. - seed atop dense litter mat). Once the plants have established, shade density due to trees and shrubs overhead is likely the main determinant of success in growth and reproduction (Cole and Weltzin 2004; Flory, Rudgers et al. 2007). Thus, areas where the litter has been removed and shrub strata are lacking, leaving seeds in contact with soil and with the benefit of higher light levels, tend to feature the densest infestations of *M. vimineum* (Barden 1987; Scholz and Byfield 2000; Glasgow 2006). It remains to be shown, however, to what extent the interaction between shade density and litter depth in intact forests may hinder population expansion of *M. vimineum*.

In order to clarify the limitations placed on *M. vimineum* populations by these local factors, a seeding experiment was carried out during the summer of 2007 with various treatments of shade and leaf litter disturbance. By planting seeds in a marginal habitat for stiltgrass survival, the experiment was designed to uncover the thresholds of

limitation that would not be apparent in more favorable habitats. The following hypotheses were examined:

1) *M. vimineum* seeds will exhibit lower levels of germination, survival, growth and fecundity when shade from subcanopy trees and shrubs is present.

2) *M. vimineum* seeds will exhibit lower levels of germination, survival, growth and fecundity when sown under deeper layers of leaf litter, with even lower survival and growth when seeds are sown on top of undisturbed litter.

Methods

Experiments were carried out at the Somerset County Sourland Mountain Preserve in Hillsborough, NJ (40°28'45" N, 74°41'45" W). The area of the preserve chosen for the study supports mature mixed hardwood forest with little exotic plant invasion. Maps from 1890 (Cook and Vermeule 1889) show that the area has been forested at least since then. Tree species present included primarily *Quercus alba* and *Q. rubra*, *Liriodendron tulipifera*, *Betula lenta*, *Fagus grandifolia*, and *Acer saccharum*. The dominant shrub within the plots was a native (*Lindera benzoin*), with a few scattered individuals of the non-native invasive *Berberis thunbergii*. Other co-occurring species included *Hamamelis virginiana*, *Cimicifuga racemosa*, and *Rubus phoenicolasius* (non-native invasive). Soils in this portion of the park are primarily Chalfont stony silt loams, on 15 to 30% slopes. Chalfont soils are weathered from argillite, and in this area are extremely stony and feature a clay fragipan at a depth of about 30cm. The argillite

(sedimentary-metamorphic rock) was created by a diabase intrusion into shales during the Jurassic period, leaving fused rock with a very low water-retention capacity. Seeds were gathered over several weeks from two local sources in the fall of 2006 (the preserve and a nearby riparian corridor), and all seeds were stored dry outdoors over the following winter.

In the spring of 2007 (May 10), three sets of plots were established at 150m intervals from each other. In an attempt to minimize variability of other biologically-significant factors, all three sets had the same aspect (east) and approximately equal slopes (15-30%). Within each set, 15 pairs of 100 cm² plots were established, where each pair contained one plot without a shrub canopy ('No Shrub') and another with a shrub canopy ('Shrub'). Since planting under any canopy gaps was avoided, tree canopy density was assumed to be approximately equal above all plots. At planting, each pair was also randomly assigned one of five litter treatments: all litter removed (Øx), litter thinned to ½ normal depth (½x), normal depth (1x), litter depth doubled (2x), and normal depth with seeds scattered on the surface (Top). The first four litter treatments were designed to test the effect of litter depth on inhibiting hypocotyl growth, while the 'Top' treatment, when compared with the '1x' treatment, would test the importance of radicle inhibition. Litter depths were determined for each set (A, B and C) by averaging the naturally-occurring depth at 10 points within the area (Mean_A = 2.5cm(±0.5), Mean_B = 1.7cm(±0.1), Mean_C = 2.3cm(±0.2)). Finally, each plot was sown with 50 seeds drawn from the pooled seeds collected in fall 2006. This density is well above levels recorded in natural subpopulations at the margin of the species' invasive range (Gibson, Spyreas et al. 2002), but is less than seedling densities commonly seen in areas with a longer history

of infestation (Cole and Weltzin 2004). In all cases except for top-sown seeds, seeds were sown in contact with the O-horizon of the soil and then covered with the appropriate depth of litter. Thus, a total of 4500 seeds were sown into 90 different plots in a split-plot design, with one of five randomly-assigned litter treatments and one of two fixed shade treatments applied to each plot.

Counts of individuals germinating and subsequently surviving were made approximately every three weeks for the rest of the summer, until the final observations were made at 130 days post-sowing. At that point, aboveground portions of surviving plants were harvested and returned to the lab for analysis. The number of leaves, spikelets and total height (basal root to tip of terminal inflorescence) of each individual were recorded, and total aboveground biomass was measured after drying in a 105 °C oven for 48h. In this species fertile seeds are produced both cleistogamously (in axillary inflorescences) and chasmogamously (on terminal inflorescence), and the measured number of spikelets includes both types pooled for each plant. Each spikelet is composed of two florets, one sterile and one fertile, so spikelet number is equal to the maximum possible number of seeds produced if allowed to mature.

The level of canopy cover over each plot was approximated in late summer by analyzing a photograph taken of the canopy over each plot. By maximizing the contrast between pixels either covered by leaves or open to the sky, a proportion of pixels covered by leaves could be calculated, and allowed a rough comparison of canopy closure. These measurements were used to verify that mean closure among the three survey areas and among litter treatments did not vary significantly. Significance was tested using one-way

ANOVAs (SAS v. 9.1; PROC ANOVA) and t-tests (PROC TTEST). The effect of both shade and litter limitations on *M. vimineum* survival over the growing season were examined using a split-plot repeated measures ANOVA (PROC GLM), where shading was the splitting factor and litter treatment was randomly applied to each pair.

Observations were taken at six time steps (23, 51, 71, 93, 118 and 130 days), and these were all used in the repeated measures analysis. Within-subject variation was tested for significance using the Huynh-Feldt adjustment to probability. Survival curves were also calculated for each combination of shade and litter treatments (PROC LIFETEST), with $n = 450$ seeds for each pairing. Log likelihood ratios were used to test for equality in survival among the pairings.

For those plants that survived to maturity, a two-way split-plot GLM was used to test for differences in height, biomass, leaf and spikelet number among treatments. As an estimate of tissue density, biomass-to-height ratio was also calculated for each surviving plant and tested in a like manner. These analyses did not include the one surviving top-sown individual, and thus only compared across the 0x, 1/2x, 1x and 2x litter treatments. Finally, with only three surviving plants under shrubs, they were discarded in a follow-up analysis, allowing for a one-way GLM analysis of the four remaining litter treatments.

Results

Experimental Design Verification

Actual canopy densities measured in late summer confirm that *a priori* categories of shade, plot and litter treatments were experimentally sound (Table 12). There was a

strongly significant difference between the mean percentage of dark pixels in the ‘Shrub’ and ‘No Shrub’ plantings, with ‘Shrub’ plots ranging from 91.03-98.73% dark and ‘No Shrub’ from 90.12-96.23%. There were no significant differences between the averages of the three sampled areas and the five litter treatments, however. In addition, mean litter depths before treatment across the three sampled areas were statistically equivalent ($F_{2,29} = 1.68, p = 0.2052$).

Survival Analysis

Overall, both deeper shade and leaf litter exhibited a strong limiting effect over the entire growing season on the survival of stiltgrass. Results of two-way split-plot ANOVAs at 3(germination), 7(establishment) and 19 weeks (survival) reveal that only litter treatment made a difference for germination success (Table 13). Shade differences were not responsible for any differences in germination: 29.7% ($\pm 2.0\%$ s.e.) of seeds germinated for ‘Shrub’ plantings and 31.6% ($\pm 2.2\%$) for ‘No Shrub.’ Differences in germination survival are entirely due to early survival of top-sown seeds being significantly lower than for the 0x and 2x treatments. As the season progresses, limitations on survival due to shade become apparent. By seven weeks after planting (approx. 3-4 post-germination), only 6.7% of the shrub-shaded individuals remained alive, while 16.3% of the ‘no shrub’ germinants persisted. By 10 weeks, survivors in both categories had again dropped in number, but losses over the remainder of the growing season were minimal. The difference between heavily- and lightly-shaded survival, however, remained significant for the rest of the growing season. Within-subject effects

were also significant in the repeated measures ANOVA (Table 14). Time of measurement had a highly significant effect throughout, and the interaction of time with both litter and shade treatments was also significant.

The resulting survival curves reinforce the above conclusions; very few plants in any litter depth treatment survived the entire growing season if planted under shrub shade (Fig. 30a). Those plants without any leaf litter survived longer into the growing season than those with some litter, but the vast majority were dead by approximately 80 days after planting. Only 2 out of 450 (and 1 from the $\frac{1}{2}x$ treatment) survived to be harvested. On the other hand, plants germinating without shrubs overhead began to stabilize after 40-50 days, and experienced fewer losses after that point, with survivors in all treatments (Fig. 30b). The effect of seed contact with the soil was explored by comparing survival curves between seeds sown on top of existing litter with those sown underneath an average litter layer depth (1x, as above). Although top-sown seedling number also stabilized between 40 and 60 days post-planting, nearly all died off in the latter parts of the growing season (Fig. 31). Only one plant out of 900 survived to harvest, and it lacked shrub shade. In contrast, although none of the 1x seeds sown under shrubs survived to the end of the season, a small number (13) of 'no-shrub' plants did. A log-likelihood comparison of all ten survival curves shown in Figures 30a and 30b yields a $\chi^2 = 750.8$, with $p < 0.0001$.

Growth and Reproduction

Although the interaction between shade and litter was not significant in the two-way survival ANOVA, it was an important source of significance for many of the growth

and reproduction variables (Table 15). For all variables except plant height, the interaction term was at least significant at $\alpha < 0.05$, and each of those overall models was even more significant. Since only 3 out of 102 survivors in the main litter treatments were shaded by shrubs, however, this analysis is not very informative. Using one-way GLMs for each variable against litter treatment only, significant results are found for every variable (Table 16). Contrast analysis reveals that significance in all cases is due to plants of the 2x treatment being larger and more robust than plants from other treatments. Closer examination of the data finds that most of the 2x survivors were from one plot in the midst of an area with very little leaf litter due to overwinter removal by water flow. Although the seeds had been covered by a twice-normal thickness of litter, many had simply grown laterally upon germination and gotten out from under the added litter before growing in earnest. When these plants are removed from the analysis, there is no significant difference for any of the variables among litter treatments (Fig. 32). The sole top-sown survivor was smaller and less productive than plants in the other treatments.

Discussion

This study expands on the findings of earlier observational studies that have shown a negative correlation between stiltgrass growth and forest shrub cover (Winter, Schmidtt et al. 1982; Horton and Neufeld 1998; Cole and Weltzin 2005), and underlines the vital importance of maintaining intact shrub layers to resist invasion. While light limitation did not affect germination, it began to cause higher mortality as the growing season continued. Ultimately, only 0.13% of seeds planted under shrubs survived, while

4.4% of those without shrub canopies were eventually harvested. Clearly, the loss of shrub layers in mature forests due to overbrowse and other factors creates an outstanding opportunity for *M. vimineum* to expand its range in North America.

Another clear result from this study is the importance of leaf litter disturbance for stiltgrass success (Oswalt and Oswalt 2007). Even up to twice-normal litter depth, growth of seeds in contact with the soil was relatively equivalent, although survival declined substantially under thicker litter. Germination, survival and growth were all very poor for those seeds that were sown on top of existing litter, however, which strongly suggests that early contact with the soil is crucial for stiltgrass establishment. The small weight of the seed presumably requires that the radicle quickly reach the soil to prevent desiccation, and even a moderately thick litter layer may thus effectively prevent establishment. The one unexpected litter treatment result was that for doubled litter depth, where the 15 surviving plants were actually as large as or larger than plants in the thinner litter treatments. This result needs a caveat, however, since 13 of those plants were planted in an area with very little natural litter. Thus, they were able to grow out laterally from under the experimentally added litter early on, and took advantage of relatively high light conditions at that plot from then on. This mirrors earlier findings of floodplain susceptibility to stiltgrass invasion, since such areas often experience leaf litter scouring during high water periods (Barden 1987; Scholz and Byfield 2000; Luken and Spath 2002).

Of greater concern to many forest managers, particularly in the northern states where stiltgrass is beginning to infiltrate, should be the loss of leaf litter thickness due to

invasion by exotic earthworms (Bohlen, Groffman et al. 2004; Hale, Frelich et al. 2005). This study illustrates that such losses might be removing one of the primary barriers to successful stiltgrass establishment in mature forests. Unless the litter layer loss occurs under very dense canopy shade, it will likely provide suitable habitat for stiltgrass to gain a foothold if seeds disperse into the area.

Also curious in this study compared to others is the low percentage of germination ($\approx 30\%$) overall. Other authors have found initial germination rates from 30-90% in the first year after planting (Gibson, Spyreas et al. 2002; Judge 2006). The low rate seen in this study could be due to a later start than wild plants in the region, or to significant seed mortality due to overwintering desiccation, as the seeds were stored dry in near-ambient temperatures. These same factors may also explain the smaller size of sown plants than wild plants growing in the vicinity of the plots, which were visually more robust (J. Schramm, personal observation). The late start (early May) might be especially important in terms of the experimental plants missing the time of greatest light availability in the herbaceous layer, as well as high sustained levels of litter and soil moisture. The missed opportunity to establish a more robust root system may have been especially influential on mid-season desiccation rates. At the time of sowing, *M. vimineum* growing in other portions of the park had not yet germinated, or had just emerged in scattered cases. At the time of first observation (3 weeks), though, wild individuals were already taller than the experimental ones, indicating that they were behind the mean germination time somewhat. Thus, by the time the sown seeds germinated (mid to late May), they may have missed a week or two of growth in which the tree and shrub canopies were not at their fullest extent. In addition, although

precipitation and temperature were close to their 30-year averages through most of the summer (National Weather Service), May was substantially drier than the average (-6.4cm). This dry period may have killed a number of plants after germinating, but before establishing a sufficient root system. Late August and particularly September were also very dry in the study year (-7.9cm off average), and may have contributed to some late season mortality or at least growth reductions for survivors.

Viewed in terms of population demographics, this study illustrates the barriers to *M. vimineum* success at several transitions (Fig. 33). The importance of soil contact was shown by the poor survival and growth of ‘Top’ seeds as compared to ‘1x’ seeds. Even though both treatments had a normal litter depth, far fewer of the ‘Top’ seeds survived through the first few weeks, an effect that was probably exacerbated by the small drought in May. They survived at comparable rates through the midsummer, but again, far more of the ‘Top’ individuals died when the weather turned dry in late August, indicating that they had not established an extensive enough root system to buffer against a lack of rainfall. The difference in survival among litter depth treatments, with a trend towards decreasing survival with increasing depth, shows the detrimental effect of delayed emergence from under deeper litter layers on *M. vimineum*. In contrast, light limitation did not have a strong effect until later in the season, indicating that the species can germinate and establish in a wide range of light conditions. Eventually, though, shade from multiple forest strata will exclude the species and prevent most survivorship and reproduction. In short, light limitation is the primary constraint on the species’ survival, but intact litter layers also limit the species’ establishment and subsequent spread.

Table 12. Summary of mean canopy density (measured as ‘% Dark Pixels’ in photo) above *M. vimineum* plantings in three plot locations and in various shade and litter treatments.

	<i>n</i> (Plantings)	Mean % Dark Pixels	S.E. % Dark Pixels	Statistical Significance
Shrub Shade	45	94.464	.278	2-sample <i>t</i> -test: <i>t</i> = 2.669, <i>p</i> = .0091
No Shrub Shade	45	93.501	.230	
Area A	30	93.540	.342	1-way ANOVA: <i>F</i> = 1.45, <i>p</i> = .2408
Area B	30	94.256	.322	
Area C	30	94.152	.300	
Litter: ∅	18	93.123	.459	1-way ANOVA: <i>F</i> = 1.45, <i>p</i> = .2242
Litter: ½x	18	94.219	.393	
Litter: 1x	18	94.402	.396	
Litter: 2x	18	94.076	.372	
Litter: Top	18	94.093	.440	

Table 13. Two-way split-plot ANOVA results for germination and survival variables in *M. vimineum* plots in relation to their shade ('No Shrub' or 'Shrub') and leaf litter (Øx, ½x, 1x, 2x, 'Top') treatments.

	<i>df</i>	Germination (3 weeks)	Establishment (7 weeks)	Final Survivorship (19 weeks)
Overall Model	19, 89	***	**	ns
Shade	1	ns	***	**
Litter	4	***	ns	ns
Shade * Litter	4	ns	ns	ns

'ns' = not significant; Significance at $\alpha < 0.05 = *$, $< 0.01 = **$, $< 0.001 = ***$

Table 14. Repeated measures ANOVA results for *M. vimineum* survival under two shade treatments and five litter treatments. Significance values for within-subject variation are adjusted by the Huynh-Feldt protocol.

B/w						
Subjects	litter	shade	litter*shade	plot	plot*litter	
	*	**	ns	ns	ns	
W/in				time*litter	time*litter	
Subjects	time	time*litter	time*shade	*shade	time*plot	*plot
	***	**	*	ns	***	ns

'ns' = not significant; Significance at $\alpha < 0.05 = *$, $< 0.01 = **$, $< 0.001 = ***$

Table 15. Two-way split-plot GLM results for growth and reproduction variables of surviving *M. vimineum* plants in relation to their shade ('No Shrub' or 'Shrub') and leaf litter (Øx, ½x, 1x, 2x) treatments.

	<i>df</i>	Height	# of Leaves	Biomass	Biomass: Height	# of Spikelets
Overall Model	11,101	ns	**	***	***	***
Shade	1	ns	ns	ns	ns	ns
Litter	3	ns	ns	*	*	ns
Shade x Litter	1	ns	*	*	**	*

'ns' = not significant; Significance at $\alpha < 0.05$ = '*', < 0.01 = '**', < 0.001 = '***'

Table 16. One-way GLM results for growth and reproduction variables of surviving *M. vimineum* plants in relation to their leaf litter (0x, ½x, 1x, 2x) treatments. Means between treatments were compared using Tukey's honestly-significant-differences, with significance at $\alpha < 0.05$. Degrees of freedom for each model were 3, with a total of 98.

	Height	# of Leaves	Biomass	Biomass:Height	# of Spikelets
Litter Depth	**	*	***	***	***
Multiple Comparisons	2x > ½x= 0x= 1x	2x > ½x	2x > 0x= ½x= 1x	2x > 0x= ½x= 1x	2x > 0x= ½x= 1x

'ns' = not significant; Significance at $\alpha < 0.05$ = '*', < 0.01 = '**', < 0.001 = '***'

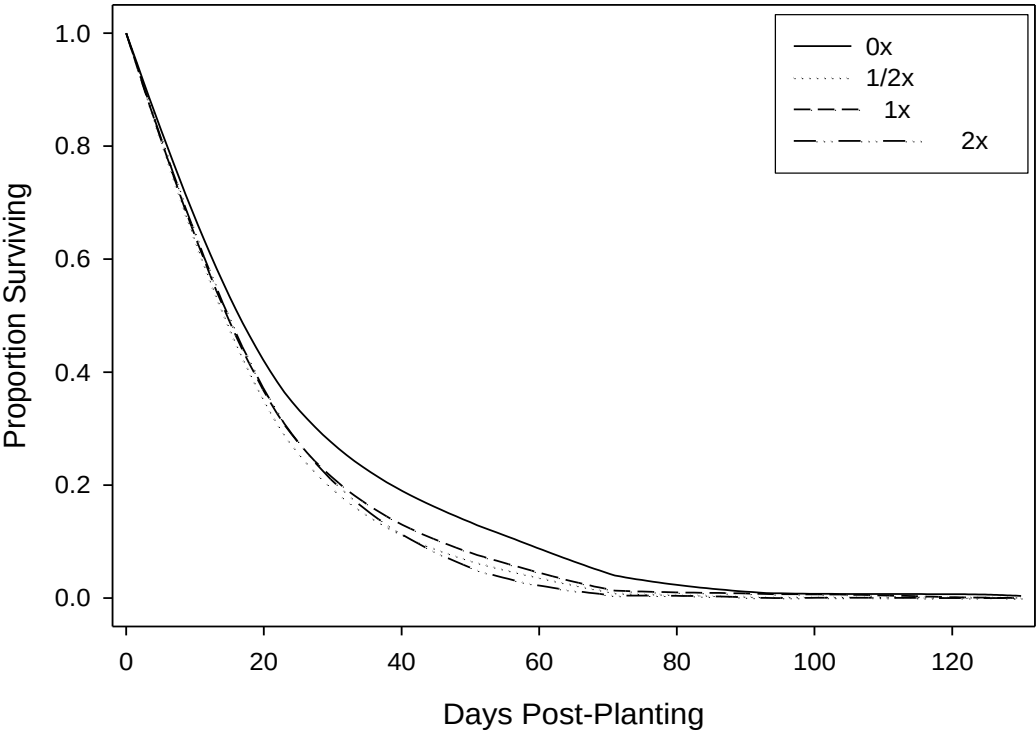
Fig. 30. Survival curves of germinating *M. vimineum* seeds planted under different litter layer treatments (0x, ½x, 1x and 2x), and all under mature hardwood canopies. (a) plots were also shaded by a shrub layer. (b) plots lacked overhead shrub layers.

Fig. 31. Survival curves of germinating *M. vimineum* seeds planted either below (bottom) or above (top) a normal thickness of leaf litter. All plots were under mature hardwood canopies, but ‘Shrub’ plots also had shrub layers present while ‘No Shrub’ plots did not.

Fig. 32. Effect of litter treatment on average growth and reproduction of planted stiltgrass seeds. Bars show standard error. Numbers above each treatment indicate the number of plants surviving until harvest (out of 900/treatment). Due to its small surviving sample, ‘Top’ treatment was not compared statistically to the other treatments, and is only shown for the purpose of comparison.

Fig. 33. Conceptual model of *M. vimineum* demographic stages (circles) and transitions (solid arrows). Habitat parameters (squares) that influence each transition are shown with dashed arrows. This study examined transitions from germination to presumptive seed production.

(a)



(b)

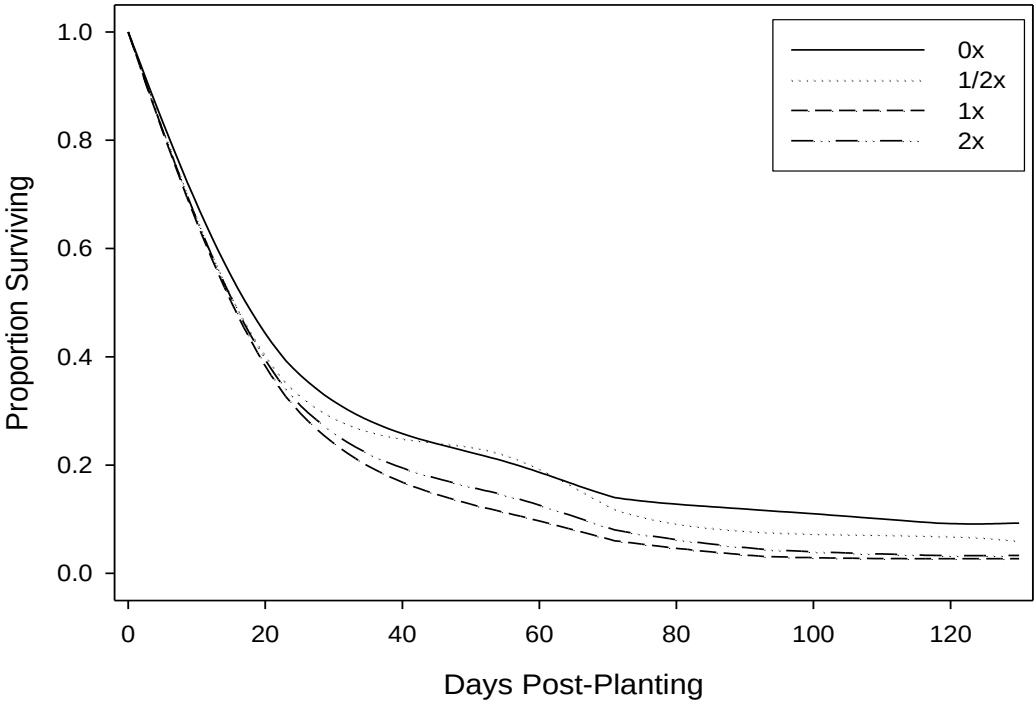
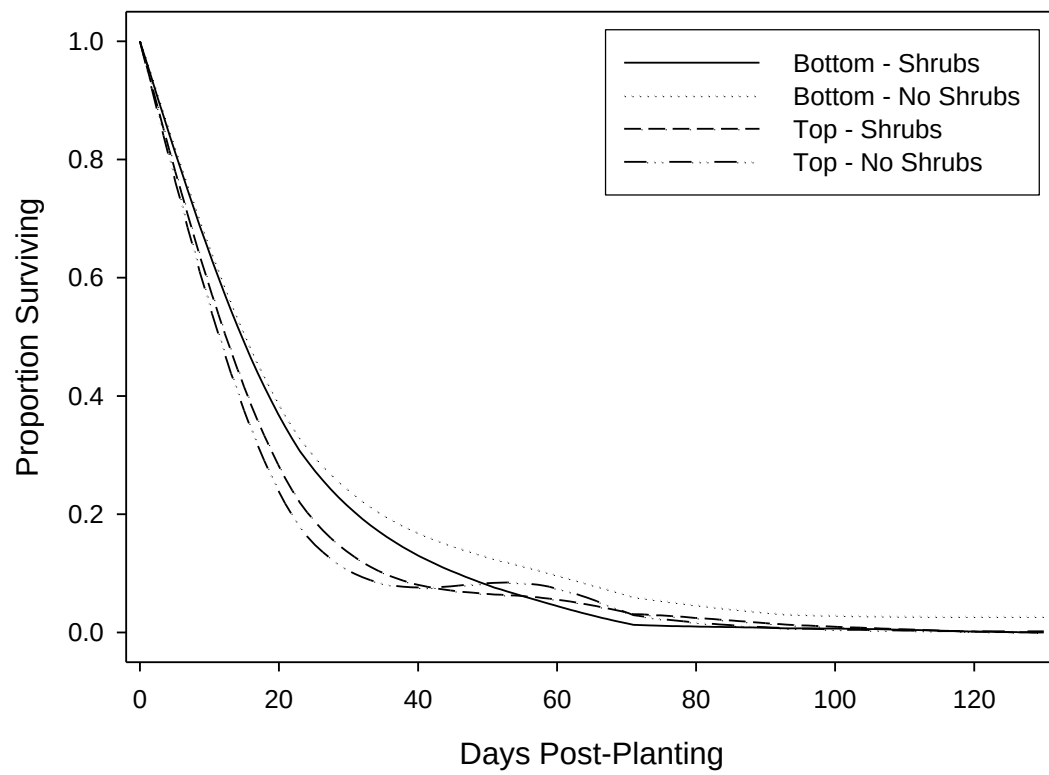
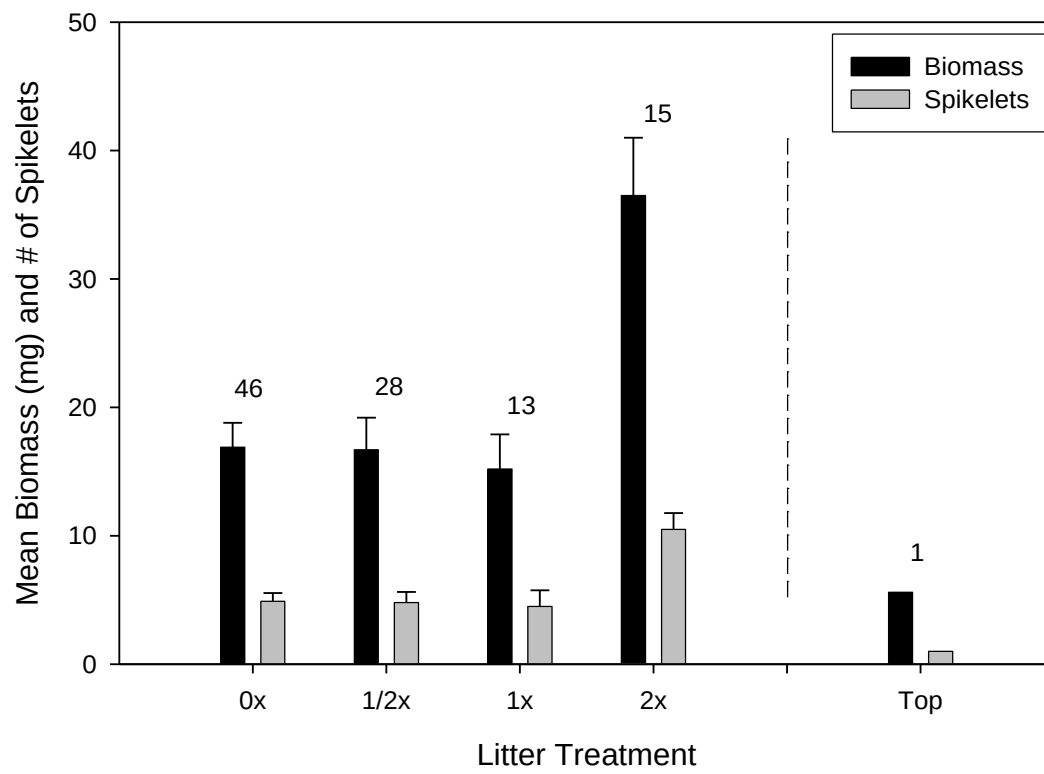
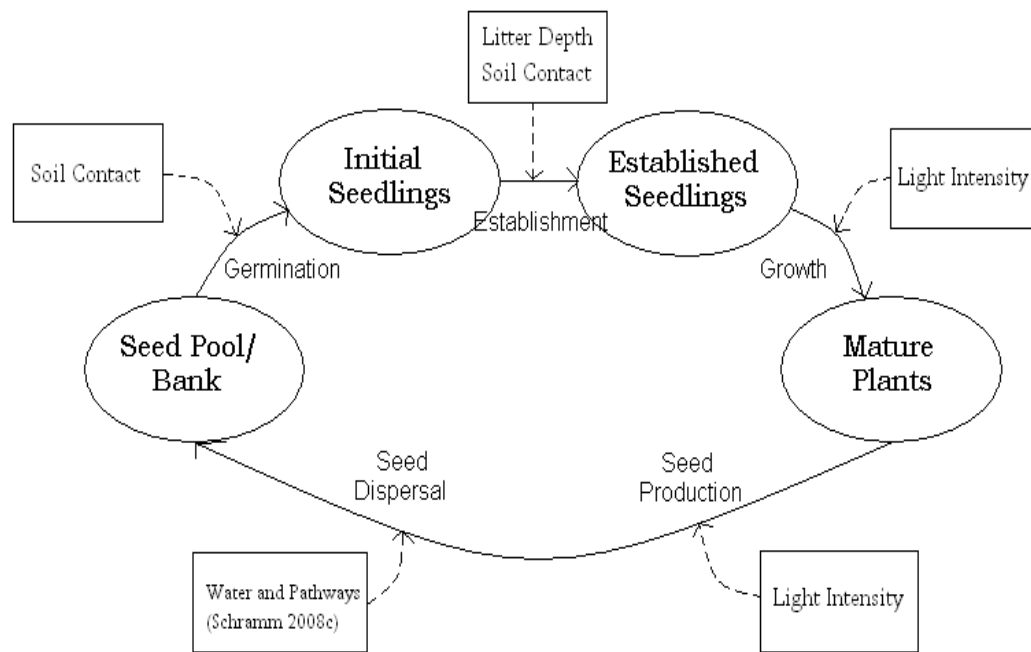


Figure 30

**Figure 31**

**Figure 32**

**Figure 33**

CONCLUSION

This study highlights the importance of many factors for the success of *M. vimineum* invasion, chief among them light limitation by tree canopies and understory shrubs, the location of dispersal corridors, and underlying soil conditions. Yet the most influential descriptor, perhaps because it encompasses all of the others to some extent, is simply the age of the forest being invaded. Young forests were consistently more heavily invaded than older forests, with the exception of those young stands that were heavily invaded by several shrub species (*Berberis thunbergii*, *Rubus phoenicolasius*, *Rosa multiflora*). In addition, factors that limited *M. vimineum* invasion most effectively were different between young and old forests. Specifically, dispersal corridors and canopy gaps enhanced invasion in old forests more than they did in young forests, while shrub cover and underlying soil sera were more influential in young stands. These data point to the confluence of land use legacies and community formation on an invasive species distribution, where subsequent maturation of a community may not effectively restrict the invasion of disturbance-tolerant species if other edaphic legacies of agricultural land use are also present. Knowledge of a community's age and development at the time of an initial invader introduction can thus explain a great deal of the variability in its eventual distribution.

In addition, this study also illustrates the vital importance of local environmental conditions for *M. vimineum* invasion. The species is especially dependent on dispersal corridors such as roads and streams to provide entry into a habitat, with waterways creating particularly extensive patches of invasion. Without such pathways, the species

disperses only short distances, mostly less than 1m per year, which is certainly not far enough to account for its very rapid expansion in the region over the last 50 years. Many patches were found without an apparent connection to dispersal corridors, however, which suggests that some form of zoochory is also occurring. Both epi- and endo-zoochory are plausible (Pakeman *et al.* 2002, Will *et al.* 2007), and one of the primary vectors in either case would be contemporaneously-growing populations of white-tailed deer (*Odocoileus virginiana*).

As one of the primary consumers of many understory shrub species in the region, deer are also influencing *M. vimineum* success in another way (Rooney *et al.* 2004, Griggs *et al.* 2006). By removing the primary competitor with *M. vimineum* for light, deer are directly enhancing the species' survival and expansion in forest settings, as seen in the planting experiment. Furthermore, the loss of shrub layers in many forests is accelerating a reduction in leaf litter depth, both by a reduction of more recalcitrant litter production and an increase of wind movement which can carry away much of the litter (Dighton 2000). This depth reduction is especially important for *M. vimineum* germination success, and is also likely to increase the population sustainability of the species. Non-native invasive earthworms are another confounded influence on litter, since they decompose native litter faster by virtue of their foraging strategy (Bohlen *et al.* 2004), also enhancing *M. vimineum* expansion.

It is clear that control and management of this species are intricately linked to other management issues in the region, particularly deer browse and overpopulation. Without active management of this herbivore in areas of high population density, efforts

to remove or control *M. vimineum* are unlikely to prove lasting (Pedersen and Wallis 2004). In areas where deer are not a major problem and *M. vimineum* invasion is not yet extensive, however, there is much hope that further invasion of the species can be limited. By focusing on points of introduction via the primary dispersal corridors, propagule spread can be contained and populations limited. In all forests, but particularly older ones, special attention should be paid to canopy gaps, since sizeable populations can form there relatively quickly. And at the landscape scale, a reasonable expectation of invasion intensity in a particular stand can be obtained sight unseen by examination of old aerial photos to determine the approximate age and history of the community. This could prove especially useful as a preliminary sorting tool in the selection of possible conservation reserves.

In the broader ecological context, this study adds to the ongoing exploration of community assembly and historical legacies by illustrating that land use effects have a dramatic influence on community invasibility. Deeper understanding of biological invasions can be gained by considering the prior condition of communities, since invasive species may have interacted very differently with native components at that time than they do under contemporary conditions. The interactions are complex, though, as disturbance events and pressures are also changing, and in many cases intensifying, synchronously with community development. These disturbances, both natural (i.e.-deer browse) and anthropogenic (i.e.- forest fragmentation and road building), can again alter the competitive interactions of native and non-native species. In most cases, these alterations effectively return the community to an earlier successional arrangement, at

least in terms of some descriptors. This can be a boon for disturbance-tolerant invasive competitors, such as *M. vimineum*.

Appendix A. Presence of tree species found at all sites in this study. Footnotes include those species seen only rarely.

Young Stands	ACPL	ACRU	ACSA	BELE	CACA	CACO	CAOV	CATO	COFL	FAGR	FRAM	FRPE	JUNI	JUVI	LITU	NYSY
Somerset-North		x		X		X	x		X	X	x		x	X	x	X
Somerset-South		x		x		x	x		x		x			x	x	x
Montgomery		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Mt. Church		x	x	x	x	x	x	x	x	x	x				x	x
McBurney		x		x			x			x	x	x		x	x	
Hunterdon		x		x	x		x		x	x	x			x	x	x
Rock Rd.		x	x	x	x	x	x			x	x			x	x	
Lambertville	x	x	x			x	x	x	x	x	x	x	x	x	x	x
Baldpate-West		x	x	x	x	x	x	x	x	x	x	x			x	
Baldpate-East		x	x	x		x	x	x	x	x	x	x	x	x	x	x
Total	1	10	6	9	5	8	10	6	8	9	10	5	4	8	10	7
Young Stands	OSVI	PATO	PODE	PRAV	PRSE	QUAL	QUBI	QUPA	QUPR	QURU	QUVE	SAAL	TIAM	ULAM	ULRU	
Somerset-North			x	x	x	x	X	x		x	X	x	x	X	X	
Somerset-South						x		x		x		x		x		
Montgomery			x		x	x		x		x		x	x	x	x	
Mt. Church						x		x		x		x	x	x	x	
McBurney			x			x		x			x	x		x		
Hunterdon			x	x	x	x		x	x		x	x	x	x	x	
Rock Rd.			x	x	x	x		x		x	x	x		x	x	
Lambertville		x			x	x		x		x	x	x		x	x	
Baldpate-West		x				x			x	x	x	x	x		x	
Baldpate-East					x			x		x	x	x			x	
Total	0	2	5	3	6	9	1	9	2	8	7	10	5	8	8	

Others: *Ailanthus altissima* (Somerset-North), *Amelanchier canadensis* (Hunterdon, Lambertville), *Betula allegheniensis* (Montgomery)

Old Stands	ACPL	ACRU	ACSA	BELE	CACA	CACO	CAOV	CATO	COFL	FAGR	FRAM	FRPE	JUNI	JUVI	LITU	NYSY
Somerset-North	X	X	X	X	X	X	X	X	X	X	X	X			X	X
Somerset-South		X	X	X	X	X	X	X	X	X	X	X			X	X
Montgomery		X	X	X	X	X	X	X		X	X				X	X
Mt. Church		X	X	X	X	X	X	X		X	X	X			X	X
McBurney		X	X	X	X	X	X	X		X	X				X	X
Hunterdon		X	X	X	X	X	X	X		X	X	X			X	X
Rock Rd.		X		X	X	X	X	X	X	X	X	X			X	X
Lambertville		X	X	X	X	X	X	X	X	X	X				X	X
Baldpate-West	X	X	X	X	X	X		X	X	X	X				X	
Baldpate-East		X	X	X	X	X	X	X	X	X	X		X		X	X
Total	2	10	9	10	10	10	9	10	6	10	10	5	1	0	10	9

Old Stands	OSVI	PATO	PODE	PRSE	QUAL	QUBI	QUPA	QUPR	QURU	QUVE	SAAL	TIAM	ULAM	ULRU
Somerset-North	X			X	X		X	X	X	X	X	X	X	
Somerset-South					X				X	X	X	X	X	
Montgomery	X		X		X		X		X	X	X		X	
Mt. Church					X		X		X	X	X	X		
McBurney			X		X		X		X	X	X	X	X	X
Hunterdon	X			X	X		X		X	X		X	X	X
Rock Rd.					X		X		X	X	X			
Lambertville	X				X	X	X		X	X		X		X
Baldpate-West		X		X	X			X	X	X	X	X	X	
Baldpate-East					X		X	X	X	X	X	X	X	
Total	4	1	2	3	10	1	8	3	10	10	8	8	7	3

Others: *Ailanthus altissima* (Baldpate-West), *Betula allegheniensis* (Montgomery), *Celtis occidentalis* (Somerset-North), *Cornus kousa* (Baldpate-West), *Platanus occidentalis* (Montgomery, Rock Rd.), *Tsuga canadensis* (Rock Rd.)

Appendix B. Presence of shrub species in sites used in this study. Footnotes include species found only rarely.

Old Stands	BETH	CACA	CEOR	ELUM	EUAL	HAVI	ILVE	LIBE	LIVU	OSVI	ROMU	RUAL	RUOC	RUPH	SMRO	Vacc.	VIDE	VIPR
Somerset-North	X	X	X		X	X	X	X		X	X			X	X			X
Somerset-South	X	X			X	X		X	X		X			X	X			X
Montgomery	X	X		X		X	X	X		X	X	X	X	X	X	X		X
Mt. Church	X	X	X	X		X	X	X		X	X	X		X	X	X		
McBurney	X		X			X	X	X			X			X	X			X
Hunterdon	X	X				X	X	X		X	X	X	X	X	X	X		X
Rock Rd.	X			X		X		X			X	X		X	X	X		X
Lambertville	X	X				X		X		X	X	X		X	X	X		X
Baldpate-West	X	X		X	X	X		X	X		X	X	X	X				
Baldpate-East	X		X	X	X	X		X		X	X	X		X	X			X
Total	10	7	4	5	4	10	5	10	2	6	10	7	3	10	9	5	0	9

Others: *Cornus kousa* (Baldpate-West), *C. racemosa* (Montgomery), *Physocarpus opulifolius* (Montgomery), *Sambucus canadensis* (Montgomery), *Staphylea trifolia* (Lambertville), *Viburnum acerifolium* (Lambertville, Baldpate-West), *V. sieboldii* (Baldpate-West)

Young Stands	BETH	CACA	CEOR	ELUM	EUAL	HAVI	ILVE	LIBE	LIVU	OSVI	ROMU	RUAL	RUOC	RUPH	SMRO	Vacc.	VIDE	VIPR
Somerset-North	X		X		X		X	X	X		X			X	X	X		X
Somerset-South	X							X	X		X			X	X		X	X
Montgomery	X		X	X				X			X	X		X	X			X
Mt. Church	X	X		X				X		X	X			X	X			X
McBurney	X	X						X	X		X			X				X
Hunterdon	X	X		X	X			X			X	X		X	X	X		X
Rock Rd.	X							X		X	X	X	X	X	X	X	X	X
Lambertville	X			X		X		X	X		X	X		X		X		X
Baldpate-West	X			X	X			X			X	X		X				X
Baldpate-East	X			X	X			X	X	X	X	X	X	X			X	X
Total	10	3	2	6	4	1	1	10	5	3	10	6	2	10	6	4	3	10

Others: *Cornus racemosa* (McBurney), *Cretaegus* sp. (Baldpate-East, Baldpate-West, Lambertville), *Viburnum acerifolium* (McBurney, Rock Rd.), *Lonicera mackii* (Somerset-North), *Physocarpus opulifolius* (Somerset-South), *Rosa palustris* (Montgomery), *Sambucus canadensis* (Mt. Church), *Spiraea* sp. (Baldpate-East, Baldpate-West), *Viburnum sieboldii* (Baldpate-East)

Appendix C. Location and ownership information for all sites used in the landscape portion of this study.

Old	Ownership	Owner	Access Point	Coordinates of Stand Center	Notes
Somerset-North	Public	Somerset County Parks	Main parking lot off of East Mountain Rd.	40° 28' 48" N 74° 42' 04" W	
Somerset-South	Public	Somerset County Parks	Main parking lot off of East Mountain Rd.	40° 27' 47" N 74° 42' 15" W	
Montgomery	Public	Hillsborough Twp.	Tiny lot on west side of Montgomery Rd., across from lg. barn	40° 26' 53" N 74° 44' 57" W	
Mt. Church	Non-Profit	D&R Greenways Land Trust	Grassy former home site on south side of Mt. Church b/w Rileyville and Stony Bk.	40° 24' 41" N 74° 47' 37" W	
McBurney	Non-Profit	D&R Greenways Land Trust	Parking lot on s. side of Mountain Rd., w. of Rileyville Rd.	40° 25' 18" N 74° 48' 03" W	
Hunterdon	Public	Hunterdon County Parks	Parking lot on CR-517 across from east end of Mt. Church Rd.	40° 25' 34" N 74° 46' 48" W	
Rock Rd.	Private	Robert Blanche	Parked at Perkowski house.	40° 23' 15" N 74° 52' 03" W	
Lambertville	Public	NJ Parks & Forestry	On Old 518 near reservoir.	40° 21' 43" N 74° 55' 02" W	Parking also at twp. park on Hewitt Rd.
Baldpate-West	Public	Mercer County Parks	Access from MCP headquarters; on north side of Fiddler's Creek Rd.	40° 19' 31" N 74° 53' 51" W	
Baldpate-East	Public	Mercer County Parks	Access from MCP headquarters; on north side of Fiddler's Creek Rd.	40° 19' 29" N 74° 53' 11" W	Or park at trailhead on Pleasant Valley Rd

Young	Ownership	Owner	Access Point	Coordinates of Stand Center	Notes
Somerset-North	Public	Somerset County Parks	Main parking lot off of East Mountain Rd.	40° 28' 41" N 74° 42' 38" W	
Somerset-South	Public	Somerset County Parks	Main parking lot off of East Mountain Rd.	40° 27' 59" N 74° 41' 50" W	
Montgomery	Public/Private	Hillsborough Twp.	Tiny lot on west side of Montgomery Rd., across from lg. barn	40° 27' 05" N 74° 44' 59" W	Two portions: downhill from parking and west of older portion
Mt. Church	Non-Profit	D&R Greenways Land Trust	Grassy former home site on south side of Mt. Church b/w Rileyville and Stony Bk.	40° 24' 45" N 74° 47' 46" W	
McBurney	Non-Profit	D&R Greenways Land Trust	Parking lot on s. side of Mountain Rd., w. of Rileyville Rd.	40° 25' 06" N 74° 48' 20" W	
Hunterdon	Public	NJ Dept. of Corrections	Park in dead-end of Featherbed Lane, east of CR-517.	40° 25' 11" N 74° 46' 00" W	On south edge of youth correctional facility (Highfields).
Rock Rd.	Private	Several owners	Parked at Perkowski house.	40° 23' 27" N 74° 51' 23" W	
Lambertville	Public	NJ Parks & Forestry	On Rocktown-Lambertville Rd, 1.5 miles east of Lambertville.	40° 21' 58" N 74° 55' 20" W	Long walk through adj. P&F parcels.
Baldpate-West	Public	Mercer County Parks	Access from MCP headquarters; on north side of Fiddler's Creek Rd.	40° 19' 30" N 74° 53' 42" W	
Baldpate-East	Public	Mercer County Parks	Access from MCP headquarters; on north side of Fiddler's Creek Rd.	40° 19' 43" N 74° 52' 50" W	

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	2006-2007	Landscape Plants I and II -Dept. of Landscape Architecture
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Research Experience	Graduate Assistant	
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Publications	Hatfield C, J Morgan, J Schramm. 2006. Wetlands Biological Indicators for New Jersey Case Study: Forested Riparian Wetlands in the Highlands of New Jersey. New Jersey Department of Environmental Protection, Trenton, NJ	
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