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Establishment, Growth, Spread, and Ecological Impacts of *Microstegium vimineum* in Central Hardwood Forests

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To the Graduate Council:

I am submitting herewith a dissertation written by Jordan M. Marshall entitled "Establishment, Growth, Spread, and Ecological Impacts of *Microstegium vimineum* in Central Hardwood Forests." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

David S. Buckley, Major Professor

We have read this dissertation and recommend its acceptance:

Ray C. Albright, Jennifer A. Franklin, Jerome F. Grant

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Establishment, Growth, Spread, and Ecological Impacts of *Microstegium vimineum* in Central Hardwood Forests

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Jordan Michael Marshall
August 2007

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ABSTRACT

Microstegium vimineum is an annual exotic grass common through the Southeastern United States. Adding *M. vimineum* to native plant communities may alter future forest composition through inhibiting the growth and influencing recruitment of seedlings into larger size classes, as well as significantly altering vertical structure and community richness, which may influence the distribution of insects.

The main objectives of these studies were to 1) establish how different mineral soil and litter disturbances, in combination with various forest canopy coverage, influence the establishment, growth, and spread of *M. vimineum*, 2) quantify effects of competition between *M. vimineum* and native hardwood seedlings, and 3) identify the influence of *M. vimineum* on insect community structure and distribution.

As percent canopy cover decreased, *M. vimineum* mean length and mean number of nodes increased. Also, as soil temperature and soil moisture increased, *M. vimineum* percent cover increased. Individual seedlings spread further from established populations in both the litter removal and the mineral soil disturbance and litter removal treatments than in the control. The apparent connection between soil disturbance and invasion by *M. vimineum* provides further impetus for careful planning and use of haul road and skid trails.

There was a reduction in *A. rubrum* and *L. tulipifera* leaf area as a result of competition with *M. vimineum*, which was likely due to competition for moisture*. Quercus rubra* did not display any differences in leaf characteristics as a result of *M. vimineum* competition. As a result of reductions in growth for *A. rubrum* and *L. tulipifera*, competitive impacts imposed by *M. vimineum* may alter the rate at which these species are recruited into larger size classes. This may change future forest composition, and have ecological and economic consequences.

In areas with *M. vimineum*, there were significantly more insects collected than in areas without *M. vimineum*. These increases in abundance likely resulted from 2.5 times greater plant cover due to the addition of *M. vimineum* to the plant communities. However, it should be noted that focusing on a single taxonomic group, such as insects, might not provide an adequate measure of exotic species impacts.

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CHAPTER I

INTRODUCTION

Exotic species, also known as introduced or alien species, are any species transported from their native range into a new range through the influence of humans (Martin and Hine, 2000). These introduced species do not necessarily impose ecological impacts on native species or ecosystems. The tens rule suggests that 10 percent of species imported will appear in the wild, 10 percent of those introduced will become established, and 10 percent of those established will be come a pest (Williamson and Fitter, 1996). While a broad generalization that often requires numerous caveats, the tens rule has been supported in aquatic systems, where 9 percent of established exotic species in the Great Lakes have had substantial detrimental effects (Mills et al., 1993), and also in some terrestrial systems (Williamson and Brown, 1986; Williamson, 1993).

Even with some supporting evidence, the tens rule does not apply in some situations, such as with the introduction of vertebrates or introductions made to small remote islands. Gaston et al. (2003) suggested that the tens rule over estimated the actual number of introduced species to an isolated Atlantic island. Also, approximately 50 percent of established, introduced vertebrates in North America become pests, greatly exceeding the tens rule (Jeschke and Strayer, 2005).

The tens rule does provide some insight and estimation of the volume of introduced species that actually impose ecological or economic harm. In general, it is usually accepted that a small fraction of all organisms introduced to North America actually impose harm to ecological and economic systems.

However, those that do cause detrimental impacts do so at such a large cost economically that understanding the true impacts and ecology of each species may alleviate some of the costs for controlling these species by limiting the unnecessary application of control for species that are not detrimental.

Estimated annual costs of exotic species in the United States have exceeded $136 billion, with over $9 billion directed annually to the control of exotic plant species (Pimentel et al. 2000). In Tennessee, two departments that would be expected to have contact with exotic species have recently received increases in appropriations. The Department of Agriculture [TDA] received increases of $3.02 million in fiscal year 2005-2006 and $3.25 million in fiscal year 2006-2007 in appropriations for operational funds, much of which was allocated towards agriculture resources conservation funds (State of Tennessee, 2005, 2006). The Department of Environment and Conservation [TDEC] also received increases in appropriations of $16.43 million and $17.31 in fiscal years 2005-2006 and 2006-2007, respectively (State of Tennessee, 2005, 2006). Of the new money available to TDEC, a total of $10.1 million, and one new position, for these two fiscal years were earmarked for the Natural Heritage program with a goal of conservation and restoration tied very closely to exotic species management (State of Tennessee, 2005, 2006). These increases in appropriations come after years of budgetary reductions for TDA and TDEC, as well as elimination of nearly 200 positions during fiscal years 2003-2004 and 2004-2005 (State of

Tennessee, 2003, 2004). These substantial reductions in dollars and personnel, even with recent increases, have made prioritization of exotic species management more important than ever to effectively control those exotic species that impose the most ecological and economic harm.

Categorical ranking systems for exotic species have been developed by agencies and organizations across the United States and the Southeast. The U.S Forest Service [USFS], National Park Service [NPS], and numerous not-for-profit organizations, such as the Tennessee Exotic Pest Plant Council [TNEPPC], have implemented ranking systems specific to the Southeastern United States and Tennessee (Table 1). Other nationally developed ranking systems are also applicable to Tennessee and surrounding states (e.g., Hiebert and Stubbendieck, 1993; APRS, 2000; Morse et al., 2004). These ranking systems all require the knowledge of how each exotic species spreads, their impacts on native plant communities and processes, and appropriate control measures available. The completeness of this knowledge heavily influences the effectiveness of these systems.

One species that is ranked in the most severe category in the TNEPPC and USFS systems, as well as receiving high ranking with the Alien Plant Ranking System, is the annual, C_4 grass *Microstegium vimineum* (Trin.) A. Camus (Poaceae) (Japanese stiltgrass, Nepalese browntop) (TNEPPC, 2001; Drake et al., 2003; Miller et al., 2004). C_4 plants use a secondary pathway to fix CO_2 into sugars by utilizing CO_2 in the mesophyll cells (Raven et al.,

Table 1. Exotic plant species ranking systems for the Southeastern United States. Ranks from TNEPPC (TNEPPC, 2001), NPS (Johnson, 1997), and USFS (USFS, 2001).

Organization	Rank	Definition
Tennessee Exotic Pest Plant Council and **National Park Service**	1 – Severe Threat	Exotic plant species that possess characteristics of invasive species and spread easily into native plant communities and displace native vegetation; includes species that are or could become widespread in Tennessee.
	2 – Significant Threat	Exotic plant species that possess characteristics of invasive species but are not presently considered to spread as easily into native communities as those species listed as Rank 1.
	3 – Lesser Threat	Exotic plant species that spread in or near disturbed areas; and are not presently considered a threat to native plant communities.
	Watch List A	Exotic plants that naturalize and may become a problem in the future. At this time more information is needed, and there is no consensus about their status.
	Watch List B	Exotic plant species that are severe problems in surrounding states but have not been reported in Tennessee.
USDA Forest Service	Category 1	Exotic plant species that are known to be invasive and persistent throughout all or most of their range within the Southern Region. They can spread into and persist in native plant communities and displace native plant species and therefore pose a demonstrable threat to the integrity of the natural plant communities in the Region.
	Category 2	Exotic plant species that are suspected to be invasive or are known to be invasive in limited areas of the Southern Region. Category 2 Species will typically persist in the environment for long periods once established and may become invasive under favorable conditions. Plant species in Category 2 pose a significant risk to the integrity of natural plant communities throughout the Region or in parts of the Region.

2005). This allows these plants to limit the time stomata remain open thus reducing water loss due to transpiration (Raven et al., 2005). Native to lowland and lower mountain forests of Japan, Korea, China, Malaysia, India, and Nepal, *M. vimineum* has spread throughout the eastern United States to as far west as Texas and as far north as New York since its first collections made in Knoxville, Tennessee, in 1919 (Fig. 1) (Fairbrothers and Gray, 1972; Sur, 1985; Osada, 1989; Hunt and Zaremba, 1992). The introduction pathway is not known for *M. vimineum*.

Previous work has established life history characteristics of *M. vimineum*, which produces similar biomass levels at light levels ranging from 18 to 100 percent full sunlight (Winter et al., 1982). This is different from other C_4 grasses, in which rapid decreases in biomass production accompany reductions in available sunlight (Winter et al., 1982; Raven et al., 2005). Adaptation to shade, which allows *M. vimineum* to efficiently photosynthesize and produce biomass, is unusual for a C_4 plant. C_4 plants are most often found in environments characterized by conditions of high temperature and high light intensities (Raven et al., 2005). *Microstegium vimineum* has shown evidence of adaptation to moist sites. While it can invade upland sites, it is more successful in mesic to hydric soils (Barden, 1987). The affinity for moist soils is another unusual characteristic of a C_4 plant. C_4 plants are usually associated with drier sites (Raven et al., 2005). This species exhibits high phenotypic plasticity in responses to both light and soil nutrient availability, which may be advantageous during invasion (Redman, 1995; Barden, 1996;

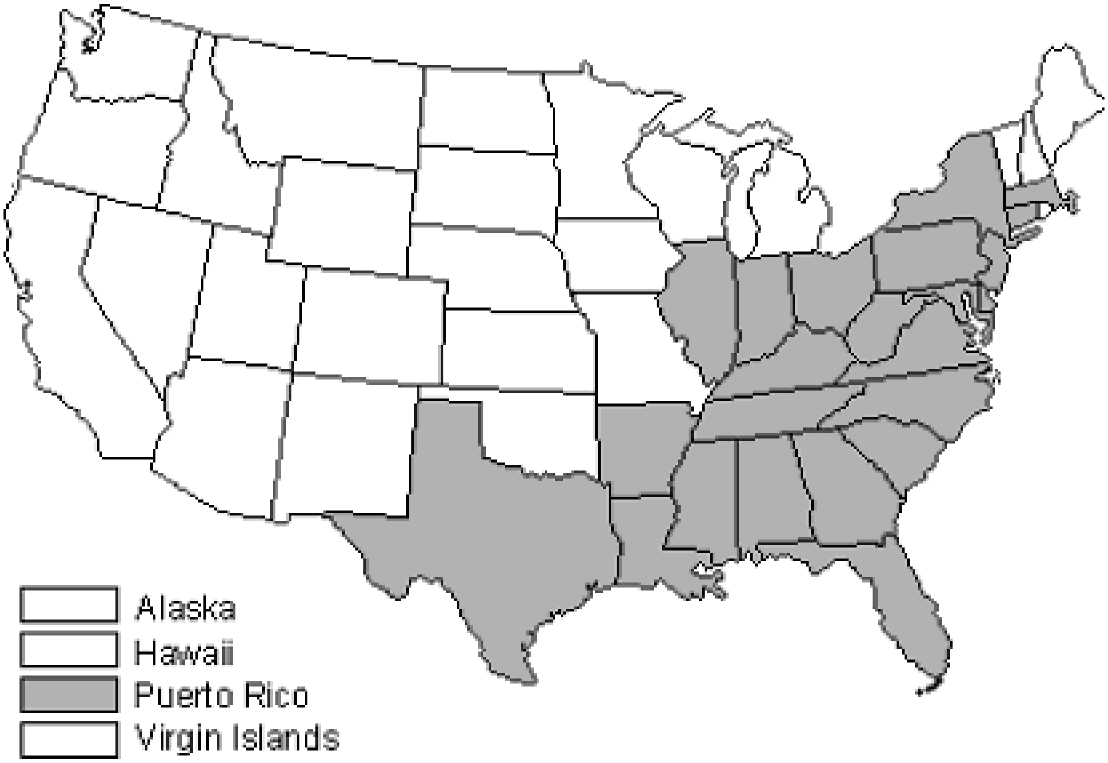


Figure 1. Distribution of *Microstegium vimineum* in the United States. Shaded States and the Commonwealth of Puerto Rico are locations of identified collections of *M. vimineum*. Note: Several states only contain 1-3 counties with known populations (USDA, 2007).

Horton and Neufeld, 1998; Williams, 1998; Cole and Weltzin, 2004, 2005). As an annual, reproduction for *M. vimineum* is solely accomplished through seed, which matures at the end of the growing season (Williams, 1998). Also, this exotic grass roots at nodes that come in contact with soil, allowing for the exploitation of resources, producing more seed bearing stems and releasing seed further from the parent population (Williams, 1998; Mehrhoff, 2000).

Previous research with other exotic species and timber management activities indicate that the light environment and seedbed properties resulting from disturbance of the forest floor and mineral soil, especially those related to silvicultural treatments, are important determinants of the establishment and spread of exotic species (Buckley et al., 2003; Setterfield et al., 2005; Webster et al., 2005). Initial invasion by an exotic species is most often facilitated by disturbance and can result in persistent, self-sustaining, and, often, growing populations (Crawley, 1989; Burke and Grime, 1996; Thompson et al., 2001).

The competitive interaction of *M. vimineum* with other herbaceous plants may alter understory vegetation (Leicht et al., 2005). However, the impacts of *M. vimineum* on hardwood seedlings may impact the individual tree species available for future recruitment into upper forest strata. Grass competition with tree seedlings can influence regeneration and tree development (Dawson et al., 2001; Gakis et al., 2004). Tree seedlings competing with grasses may have reductions in leaf size, weight, and number, as well as height and diameter measurements, compared to competition-free seedlings (Gakis et al., 2004). Roots of tree seedlings often grow deeper to avoid competition with grass roots and colonize the soil surface in the absence of grasses (Dawson et al., 2001). Such plasticity varies with species and shifts in carbon allocation, as well as biomass accumulation for root system expansion, will most likely have detrimental effects to above-ground growth.

Factors that determine the susceptibility of managed hardwood forests to invasion by *M. vimineum* and impacts of this species on native vegetation are not well understood. Barriers that may influence invasion by *M. vimineum* include impediments to seed production and dispersal, basic microsite characteristics, and competition with native vegetation. Although the distribution of this species at fine scales may be influenced by dispersal (Cole and Weltzin, 2004), seed production and dispersal are not likely to be primary barriers to invasion by *M. vimineum* of interior areas of managed Central Hardwood forests. Evidence for the lack of seed dispersal barriers includes the prolific production of long-lived seeds and personal observations of isolated stands of this species on various natural micro-topographic features, including tip-up mounds, in interior forest areas with little recent human disturbance.

Further, substantial populations of *M. vimineum* are well entrenched throughout East Tennessee along roads and in other areas with soil disturbance in forested, agricultural, suburban, and urban landscapes (Fig. 2). In contrast to seed production and dispersal, basic microsite factors and the

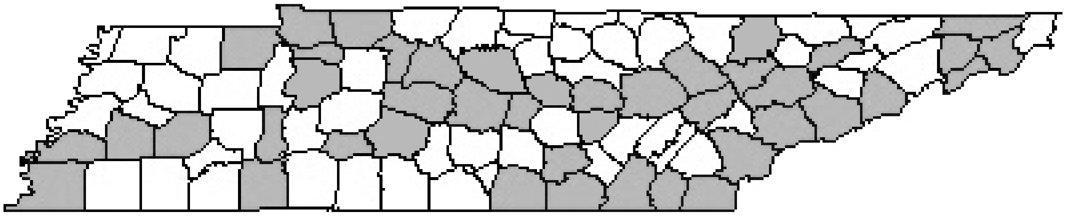


Figure 2. Distribution of *Microstegium vimineum* in Tennessee. Shaded counties are locations with documented collections of *M. vimineum* (UTH, 2007).

competitive effects of native vegetation may be more likely to limit the ability of *M. vimineum* to establish and spread within interior portions of both managed and unmanaged hardwood forests. By determining levels and combinations of basic microsite factors that facilitate *M. vimineum* invasion, managers will have a foundation for further studies concerning what areas within a forest under silvicultural management need to be targeted for control of *M. vimineum*. Chapter II deals with an investigation of the microsites created as a result of selective harvesting and the establishment and growth of *M. vimineum* in those different disturbances. Chapter III presents research related to the effects of litter removal and mineral soil disturbance within forest with intact canopies. This information will aid managers in predicting where and when *M. vimineum* will become a problem, and to make informed decisions concerning where to focus control efforts and spending.

Rigorously defining the relative competitive effects of native hardwood seedlings with different strategies and levels of shade tolerance on *M. vimineum* will be an important first step toward defining tree species components within managed forests that slow the spread of this invasive species. Simultaneous documentation of competitive effects of *M. vimineum* on native hardwood seedlings will provide information on what types of changes may occur in the composition of forest overstories as a result of recruitment inhibition due to invasion by this species. Chapter IV presents research that investigates the competitive interaction of *M. vimineum* with seedlings of three native hardwood tree species.

The addition of an exotic plant species not only alters the plant community it has invaded, but also all other communities that interact within a given ecosystem. Insect communities are closely tied and continually interact with plant communities (Haddad et al., 2001). Changes in plant richness, diversity, and cover can influence the distribution and abundance of insects (Southwood, 1977; Southwood et al., 1979; Lawton, 1983; Risch et al., 1983; Andow, 1990; Knops et al., 1999; Haddad et al., 2001; Crist et al., 2006). Alterations in insect communities may provide more information on the overall ecological impacts of *M. vimineum* within Central Hardwood forests. Chapter V deals with an investigation of the effects of *M. vimineum* on insect abundance and richness.

Increased emphasis on *M. vimineum* and other common, often dominating, exotic plant species is necessary within Central Hardwood forests. Understanding interactions of these exotic plants with native species is important ecologically, as well as economically. Future forest floral and faunal composition may depend heavily on the impacts of introduced plant species. Quantifying these impacts will aid in the prioritizing of management activities, and the general ecological understanding of plant and animal interactions.

CHAPTER II

MICROSITE FACTORS RELATED TO THE GROWTH OF *MICROSTEGIUM VIMINIEUM* AFTER SELECTIVE HARVESTING IN A CENTRAL HARDWOOD FOREST

Abstract

Disturbances related to silvicultural activities are inevitable, and may facilitate the spread of established populations of exotic species. *Microstegium vimineum* is an annual exotic grass that has spread throughout the eastern United States. Different categories of disturbances resulting from cutting and the operation of logging machines within three selective harvest blocks were identified and characterized by measuring several environmental variables. *M. vimineum* was sown within the microsites categorized. Differences in growth of *M. vimineum* in microsites subject to these different disturbances were quantified. As percent canopy cover decreased, *M. vimineum* mean length and mean number of nodes increased. Also, as soil temperature and soil moisture increased, *M. vimineum* percent cover increased. In undisturbed microsites in which *M. vimineum* was not sown, the exotic grass was not a dominant species, whereas in all other microsites created by logging machine operation *M. vimineum* was a dominant species whether those areas were sown or colonized by wild populations. *M. vimineum* percent cover was not significantly correlated with plant species diversity. This suggests that in forest stands influenced by harvesting disturbance, susceptibility to invasion by *M. vimineum* may not be limited by higher diversity. These results suggest that soil disturbance alone may be sufficient for facilitating *M. vimineum* invasion of Central Hardwood forests. The apparent connection between soil disturbance and invasion by *M.*

vimineum provides further impetus for careful planning and use of haul road and skid trails.

Introduction

Forest management activities such as harvesting and the establishment of forest roads have been suggested as factors that may facilitate exotic plant invasions (Buckley et al., 2003; Gelbard and Belnap, 2003; Johnston and Johnston, 2004; Lundgren et al., 2004; Parendes and Jones, 2000). Repeated disturbances such as those created by forest road establishment, use, and maintenance, often provide suitable habitat openings for exotic species invasion (Crawley, 1989). Changes in forest structure related to silvicultural harvesting practices and other activities might also remove barriers to successful establishment and spread (Haeussler et al., 2002; Johnstone, 1986; Silveri et al., 2001). Increased levels of photosynthetically active radiation (PAR), soil moisture, and soil compaction, as well as decreased levels of canopy cover and litter layers, may underlie removal of such barriers (Buckley et al., 2003; Hendrickson et al., 2005).

Microstegium vimineum (Trin.) A. Camus (Poaceae) is a lower montane grass species native to Japan, Korea, China, Malaysia, India, and Nepal (Osada, 1989; Sur, 1985). Since its first collections in North America made in Knoxville, Tennessee, in 1919, *M. vimineum* has spread throughout the eastern United States as far west as Texas and as far north as New York (Fairbrothers and Gray, 1972; Hunt and Zaremba, 1992). *M. vimineum* can grow under a range of light levels, with individuals retaining shade-tolerant attributes even when acclimated to high light levels (Horton and Neufeld, 1998). Barden (1987) noted that *M. vimineum* readily invades areas altered by natural and human induced disturbances and it may be well adapted for disturbances in forests through light-induced developmental plasticity (Cheplick, 2006).

Microstegium vimineum is a major concern as it receives high ranking in the US Geological Survey Alien Plants Ranking System (APRS, 2000; Drake et al. 2003). US Forest Service rankings also place *M. vimineum* in the highest category of concern (USFS, 2001). Within these rankings and other regional ranking lists such as those produced by the South Carolina and Tennessee Exotic Pest Plant Councils, *M. vimineum* is identified as possessing the ability to invade native plant communities, displace native species, and significantly alter the structure of the native community (Drake et al., 2003; Haldeman et al., 2004; TNEPPC, 2001; USFS, 2001). Oswalt et al. (2004) found that as *M. vimineum* biomass increased, northern red oak end-of-season height growth decreased. Also, as demonstrated by Cole (2006), hardwood tree seedlings are suppressed by *M. vimineum* resulting in limited seedling recruitment. Furthermore, increased visibility and spread of *M. vimineum* are common topics at meetings and gatherings of regional land managers. However, despite the high ranking of *M. vimineum* as a threat to native ecosystems and abundant concern, there is still limited understanding of what factors facilitate the establishment, growth, and spread of this species, and how these factors may increase susceptibility of forests to invasion. The ability of *M. vimineum* to compete with different species varies, and this exotic may not be as effective at crowding out other species as previously expected (Leicht et al., 2005).

Concerns over *M. vimineum* and other exotic species, combined with limited knowledge of the ecology of these species in native North American ecosystems, have prompted investigations of what ecosystem types are most susceptible to invasion and what factors influence their susceptibility to invasion. This information is essential for more targeted research and efficient management of exotic species. Kennedy et al. (2002) argued that plant diversity provides a defensive line for invasion. However, it may be more appropriate to state that plant diversity limits plant invasion barring extrinsic factors, such as disturbance (Naeem et al., 2000; Thuiller et al., 2006). Other results have suggested that areas of higher diversity are more susceptible to invasion (Stohlgren et al., 2003).

The objectives of this study were to 1) establish how different combinations of canopy cover, light, soil moisture, and soil disturbance levels encountered in forests managed with selective harvesting influence growth of *M. vimineum*, and 2) investigate relationships between plant species diversity and the presence of *M. vimineum* patches.

Methods

This study was conducted at the University of Tennessee Forest Resources Research and Education Center at Oak Ridge, TN (36°00' N, 84°13' W) in the Appalachian Ridge and Valley Region of North America. The study site is within the Appalachian section of the Central Hardwood forest, which is characterized as being an Oak-Hickory forest type (Fralish 2003). Soils are a silty clay loam and classified as ochreptic hapludults (USDA 1981). Mean annual temperature is 15° C and mean annual precipitation is approximately 1500 mm (NCDC 2005).

A selective harvest initiated in February 2005 created microsites utilized for this study. Approximately 44.2 percent basal area was removed from the original 31.2 m^2/ha during the harvest, with *Quercus alba* L. (Fagaceae) and *Liriodendron tulipifera* L. (Magnoliaceae) being the dominant species removed. Transects were established on a 10 m spacing and parallel to the long axis of each of three 2.8 ha harvesting blocks on 21-23 March 2005, immediately following the completion of harvesting. Transect lengths were variable to conform to the shape of the harvested blocks. Along each transect, all types of soil disturbance related to harvesting, as well as undisturbed areas, were recorded by category.

Disturbances were categorized as a 1-pass compacted log skid (LS), multiple-pass compacted (MPC), multiple-pass loosened (MPL), 1-pass compacted track without litter (OPT), and 1-pass compacted track with litter (OPTL). LS areas, often between bulldozer tracks, had log drag marks. Small vegetation and litter were destroyed within these drag marks. MPC and MPL areas occurred in the same areas because they were created by the same activities. Multiple-pass areas were created by repeated passes of a rubber-tired skidder, bulldozer, or both, leaving little or no vegetation or litter. Areas labeled as MPC were the compressed rut or track mark left by the machinery. MPL were characterized by much less compacted soil and were often created as the track or tire pushed soil up along sides of ruts. OPT areas were created by a bulldozer moving through and removing litter in the track marks, with litter and small vegetation essentially undisturbed between the two tracks. OPTL areas were similar to the previous category, but litter was present and covered the bulldozer track marks. The position and segment length covered by each disturbance type were recorded along each transect.

Five occurrences of each disturbance category, as well as the undisturbed category, were randomly selected within each harvesting block. OPTL plots only occurred in two of the three harvesting blocks. To ensure independence between plots, the selection protocol limited the choosing of disturbance occurrences that were spatially connected along each transect. For example, if an OPT was selected, then the second, paired track that would have been created at the same time was omitted as a potential selection. This same protocol was used for LS. If an LS was selected, then the tracks on either side were not selected. For MPC and MPL, the limited number of these disturbance types required the selection of spatially connected occurrences. In these cases, an attempt was made to maximize independence by offsetting plots 5 m perpendicular to transect.

Microstegium vimineum seed was collected 20 October 2004 from a large population, which had become established at the Ijam's Nature Center Meade's Quarry (35°57' N, 85°52' W) in Knox County, TN. After air-drying for

1 day at room temperature, seeds were separated randomly into lots of 100 and cold stratified at 4°C in polyethylene bags with 150 ml of wet sand from December 2004 until planting.

Germination and establishment tests conducted 7 March-7 June 2005 resulted in 84 percent germination and survival at a mean daily temperature of 20°C in a growth chamber. Of samples selected for germination testing, 60 percent of *M. vimineum* seeds sprouted a radical while still in cold storage at 4°C. In a previous study, Williams (1998) reported germination rates of *M. vimineum* seeds ranging from 80-90 percent. One-hundred *M. vimineum* seeds were sown within 0.25 m^2 (0.56 m diameter) plots in selected disturbance occurrences on 29-30 March and 6 April 2005 in an attempt to mimic the density of natural populations. A 0.56 m diameter ring constructed of vinyl tubing was used during sowing to delineate the 0.25 m^2 area of each plot. Use of 12 of the 85 plots was discontinued as a result of continued logging activity and disturbance in all blocks within the study area (LS = 2, OPT = 4, OPTL = 0, MPC = 1, MPL = 3, U = 2).

Mean litter depth was calculated from measurements made with a metric ruler to the nearest 0.5 cm in the center of each quadrant of the 0.25 m^2 plot on 18 July 2005. Soil compaction was measured as insertion force in the center of each 0.25 m^2 plot with a soil penetrometer as kg/cm^2 (Lang Inc., Gulf Shores AL) on 18 July 2005. Relative differences in soil moisture between planting locations were measured using a Trase Time Domain Reflectometry (TDR) probe (Soilmoisture Corp., Santa Barbara CA) with 15 cm waveguides on 18 July 2005. The date for soil moisture measurement was selected during an extended dry period, 3-4 days. Maximum differences in soil moisture between treatments are most likely to occur during periods of low rainfall. Soil temperature was measured using a 29 cm soil thermometer (Reotemp Instruments Corp., San Diego CA) inserted 15 cm into the soil on the same day that soil compaction and moisture were measured.

Instantaneous measurements of photosynthetically active radiation (PAR [μmols $m^{-2}s^{-1}$]) were obtained with an AccuPAR Linear Ceptometer (Decagon Devices Inc., Pullman WA) held at 1 m above the soil surface over the center of the 0.25 m^2 plot on a cloudless day. An identical, unattended ceptometer programmed to record and log PAR measurements every 2 minutes was placed in an open field adjacent to the harvesting blocks. These zero percent canopy PAR readings from the unattended ceptometer were utilized to calculate percent full PAR for each plot.

Canopy cover was measured with a digital plant canopy imager (CID Inc., Camas WA). The canopy imager was positioned 1 m above the soil surface over the 0.25 m^2 plot center. Percent canopy cover was calculated by CI110 computer software (Ver. 3.0.2.0, CID Inc., Camas WA). Percent PAR and percent canopy cover measurements were taken on 24 and 26 August 2005. Stem length, mean number of nodes, and mean number of seed heads of the five longest *M. vimineum* stems were measured within each plot on 12-14 October 2005.

A point intercept frame with pins arranged on a 7 cm grid (45 sample points per plot) was utilized to measure percent plant cover within each 0.25 m^2 plot on 13-15 September 2005. While some species may not have been present at this sampling time, it was assumed that the majority of plant species were sampled. Plants were identified to species, excluding species in the genera *Carex*, *Poa*, *Rubus*, and *Vaccinium*. Plant diversity was calculated for each disturbance category within the three harvest blocks. Diversity was calculated for each disturbance category as the Shannon-Weaver Diversity Index,

$$H = -\Sigma\, p_i \ln(p_i)$$

where p_i = the proportion of the *i*th species (Hayek and Buzas, 1997). The proportion of the *i*th species was calculated as (the number of pins intercepting the *i*th species)/(total number of pins intercepting all species).

For each plot sown with *M. vimineum*, a paired plot was located in un-sown area adjacent to each sown *M. vimineum* plot. Un-sown paired plots were placed 2 m away in a random direction along the same disturbance feature as the original sown plot. For plots categorized as undisturbed (U), un-sown paired plots were placed 2 m away on a random compass bearing. Point intercept measurements of cover were taken at each paired plot. Diversity was calculated for un-sown plots. For both sown and un-sown plots, *M. vimineum* was excluded from the diversity calculations. Pearson correlation was utilized to identify relationships between the presence of *M. vimineum* and plant diversity. Species dominance was calculated for sown and un-sown plots in each disturbance category as the total area covered for a given species / total area sampled.

Statistical analyses were conducted with SAS computer software (Ver. 9.1, SAS Institute Inc., Cary, NC). Multivariate regression was utilized to test for relationships between the environmental variables (soil moisture, soil temperature, soil compaction, litter depth, percent PAR, and percent canopy) and the *M. vimineum* growth variables (percent cover, mean length, mean number of seed heads, and mean number of nodes) within the study site. Variable selection for the multivariate regression was done through a stepwise procedure with $\alpha = 0.05$. Multiple linear regression was used to identify how the environmental variables selected through the stepwise procedure influenced the individual *M. vimineum* growth variables. Analysis of variance (ANOVA) was utilized, along with Tukey's HSD, to identify differences in environmental variables between soil disturbance categories.

Results

Seventy-three plots of the original eighty-five in which *M. vimineum* was sown remained for analysis after 12 were lost to additional logging disturbance, as were the corresponding paired plots (LS = 13, OPT = 11, OPTL = 10, MPC = 14, MPL = 12, U = 13). Microsite plots categorized as MPC and MPL had the lowest canopy cover and highest percent PAR and MPL plots had the lowest compaction as indicated by the lowest insertion force (Fig. 3, 4). Those plots categorized as OPTL and U had the greatest litter depth, as well as the lowest *M. vimineum* stem length and percent cover

(Fig. 5, 6, 7). Soil moisture differed significantly between MPL and OPT plots, with MPL plots having lower volumetric soil moisture (Fig. 8). Soil temperature between OPT, OPTL, LS, and U did not differ significantly (Fig. 9).

Variable selection for the multivariate regression resulted in percent canopy cover, soil temperature, and soil moisture having significant Wilks' Lambda values (Table 2). The overall model indicated that a significant relationship existed between the *M. vimineum* growth variables (percent cover, mean stem length, number of seed heads, and number of nodes) and the environmental variables (percent canopy cover, soil temperature, and soil moisture) (Table 2). Percent cover of *M. vimineum* was significantly influenced by soil temperature and soil moisture adjusting for all other variables. Increases in soil temperature and soil moisture resulted in increased *M. vimineum* percent cover ($\beta_{\text{temperature}} = 8.13$, $t = 2.75$, $p < 0.001$; $\beta_{\text{moisture}} = 2.53$, $t = 2.65$, $p = 0.01$; respectively). Mean length of *M. vimineum* stems and number of nodes decreased with an increase in percent canopy cover ($\beta_{\text{canopy}} = -1.07$, $t = -3.86$, $p < 0.001$; -0.07, $t = -4.44$, $p < 0.001$). Although the mean number of seed heads was included in the significant overall multivariate model, a significant relationship did not exist with the environmental variables.

A total of 58 plant species were encountered across all soil disturbance categories. Common plant species encountered, other than *M. vimineum*, were *Toxicodendron radicans* (L.) (Anacardiaceae) and *Lonicera japonica*

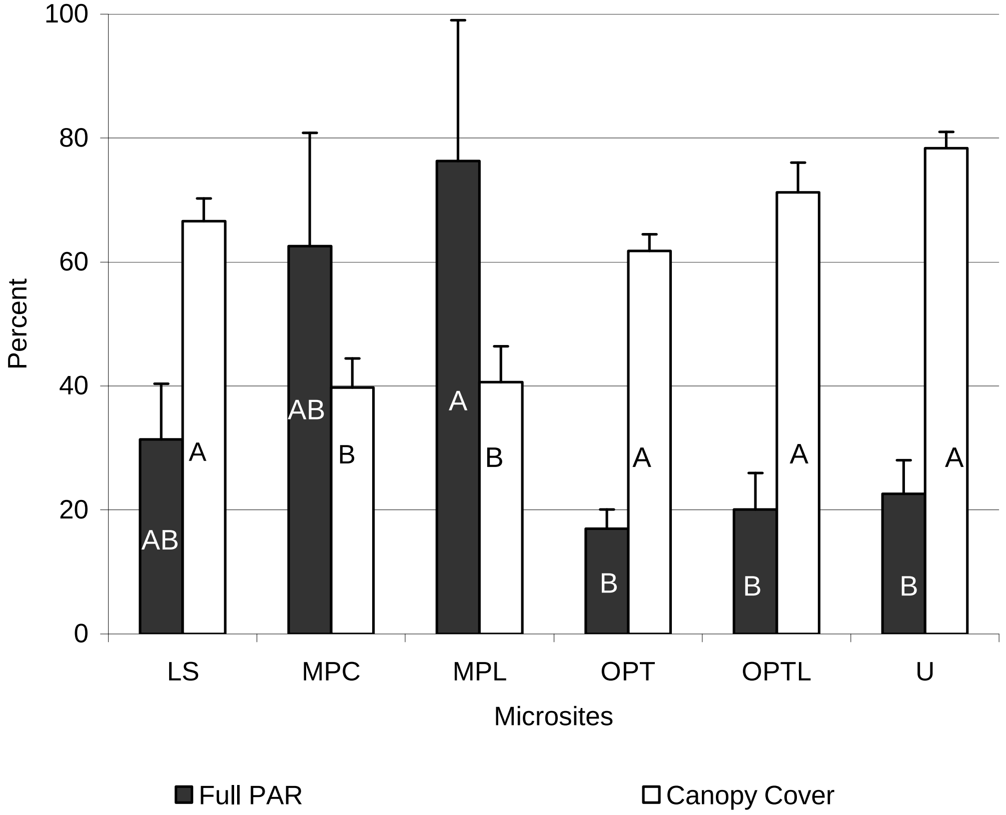


Figure 3. Percent full PAR and percent canopy cover for each microsite. Error bars represent 1 SE. Unique letters indicate significantly different microsites utilizing Tukey's HSD. LS = 1-pass log skid, MPC = multiple-pass compacted track, MPL = multiple-pass loosened, OPT = 1-pass compacted track, OPTL = 1-pass compacted track with litter, U = undisturbed.

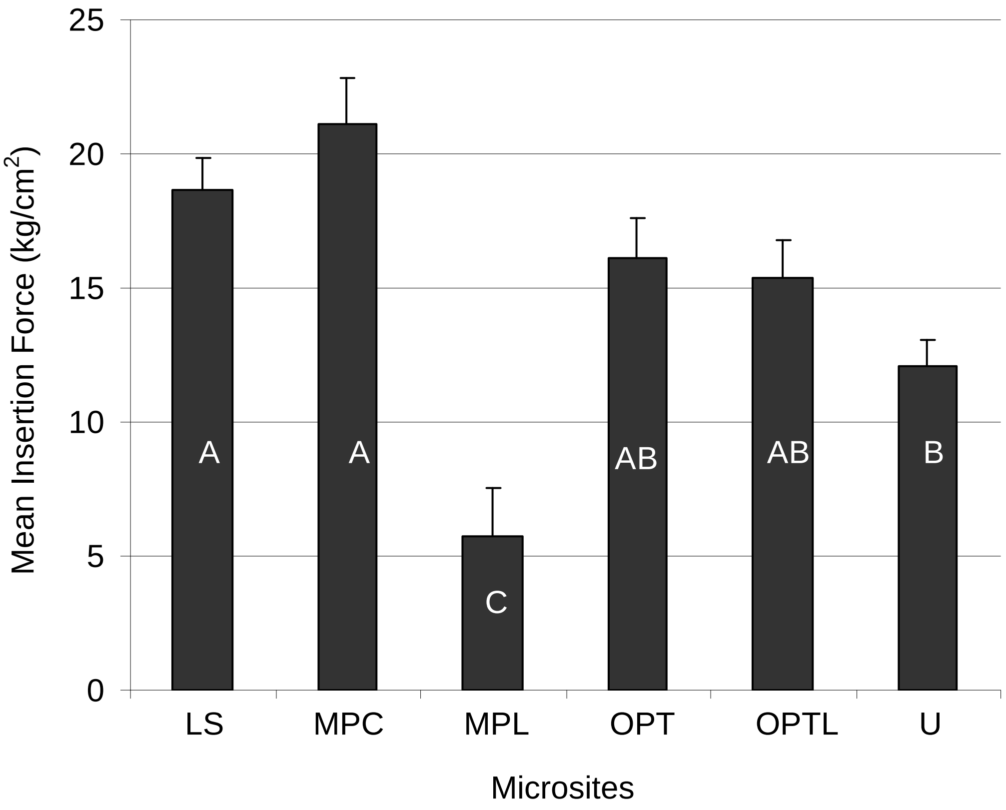


Figure 4. Soil compaction for each microsite created by harvesting machinery. Error bars represent 1 SE. Unique letters indicate significantly different microsites utilizing Tukey's HSD. LS = 1-pass log skid, MPC = multiple-pass compacted track, MPL = multiple-pass loosened, OPT = 1-pass compacted track, OPTL = 1-pass compacted track with litter, U = undisturbed.

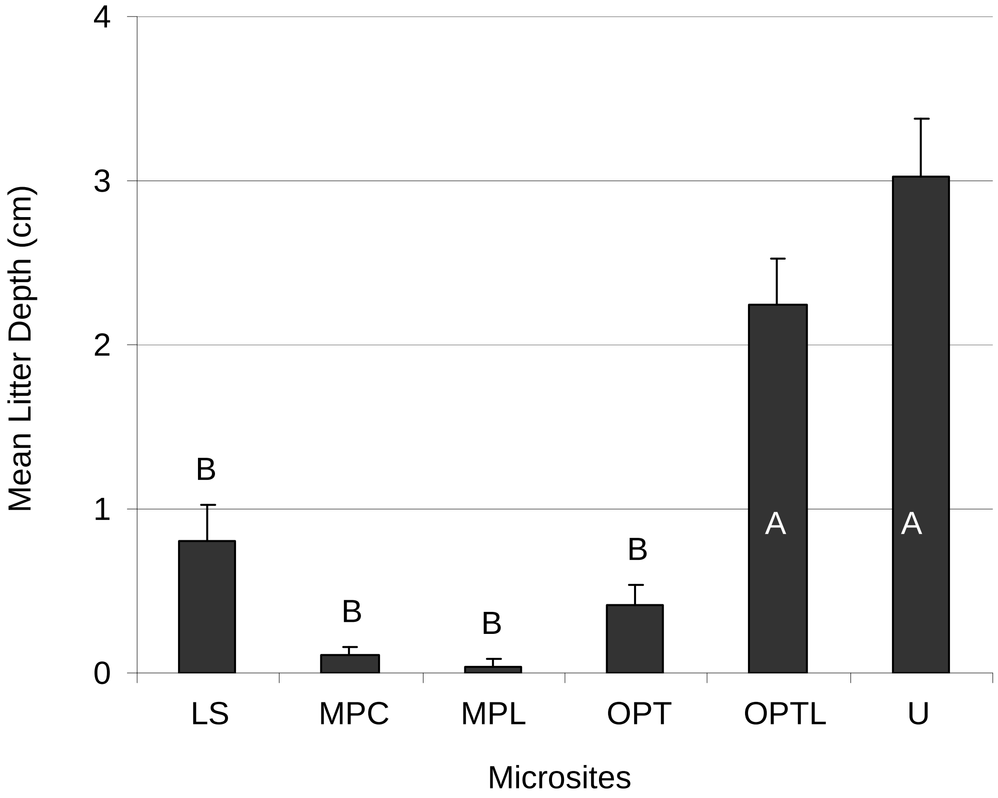


Figure 5. Mean litter depth for each microsite created by harvesting machinery. Error bars represent 1 SE. Unique letters indicate significantly different microsites utilizing Tukey's HSD. LS = 1-pass log skid, MPC = multiple-pass compacted track, MPL = multiple-pass loosened, OPT = 1-pass compacted track, OPTL = 1-pass compacted track with litter, U = undisturbed.

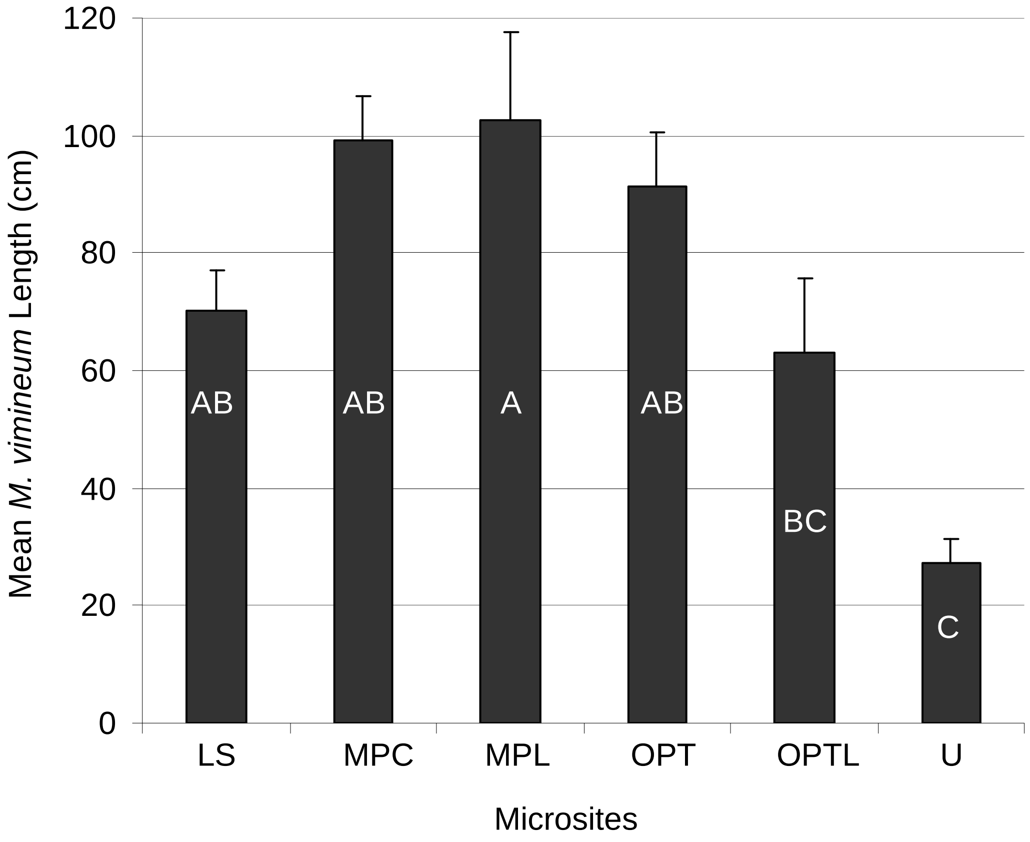


Figure 6. Mean *Microstegium vimineum* length for the five longest stems for each microsite created by harvesting machinery. Error bars represent 1 SE. Unique letters indicate significantly different microsites utilizing Tukey's HSD. LS = 1-pass log skid, MPC = multiple-pass compacted track, MPL = multiple-pass loosened, OPT = 1-pass compacted track, OPTL = 1-pass compacted track with litter, U = undisturbed.

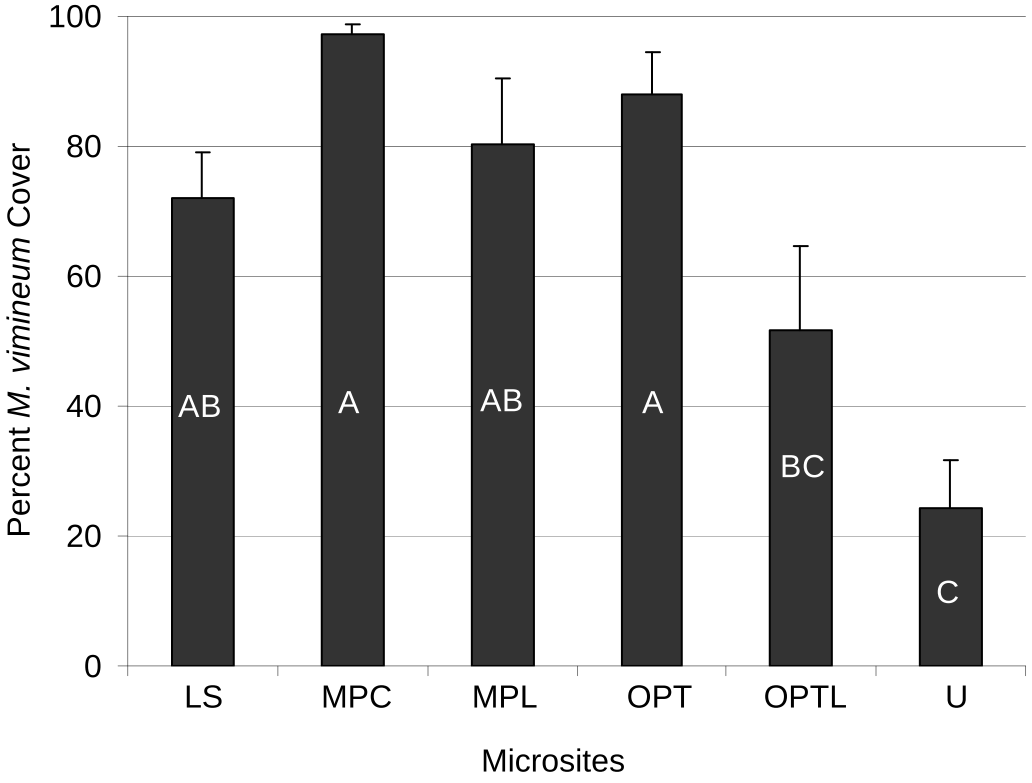


Figure 7. Percent *M. vimineum* cover for each microsite created by harvesting machinery. Error bars represent 1 SE. Unique letters indicate significantly different microsites utilizing Tukey's HSD. LS = 1-pass log skid, MPC = multiple-pass compacted track, MPL = multiple-pass loosened, OPT = 1-pass compacted track, OPTL = 1-pass compacted track with litter, U = undisturbed.

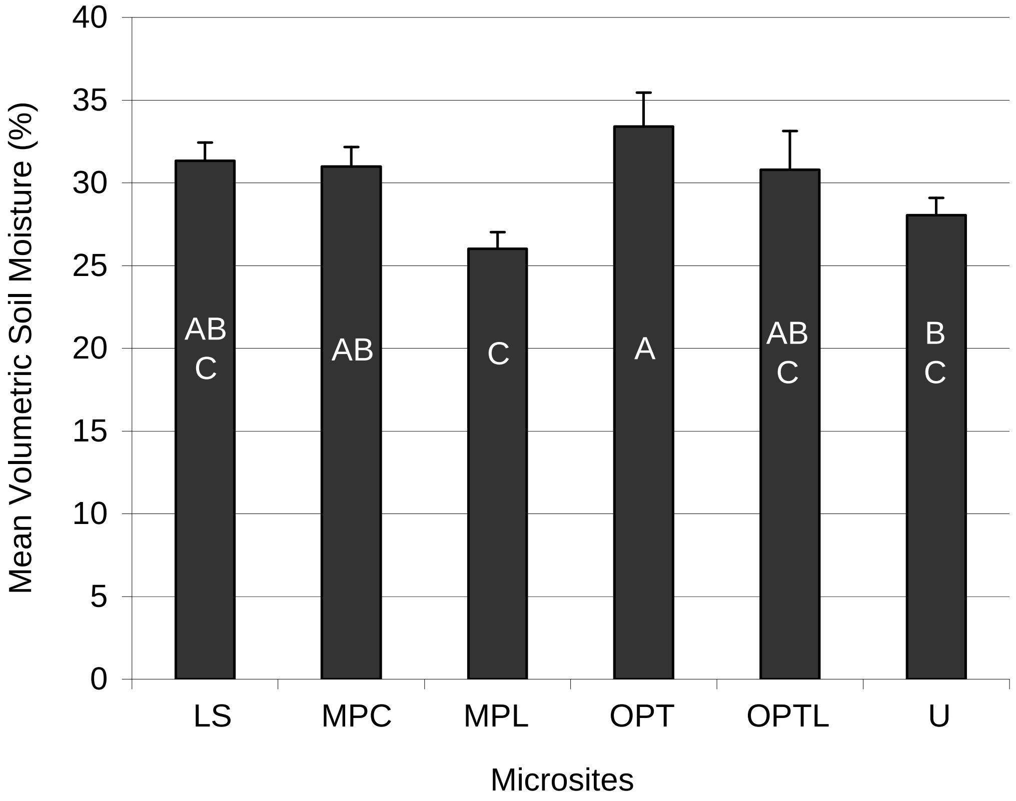


Figure 8. Soil moisture for each microsite created by harvesting machinery. Error bars represent 1 SE. Unique letters indicate significantly different microsites utilizing Tukey's HSD. LS = 1-pass log skid, MPC = multiple-pass compacted track, MPL = multiple-pass loosened, OPT = 1-pass compacted track, OPTL = 1-pass compacted track with litter, U = undisturbed.

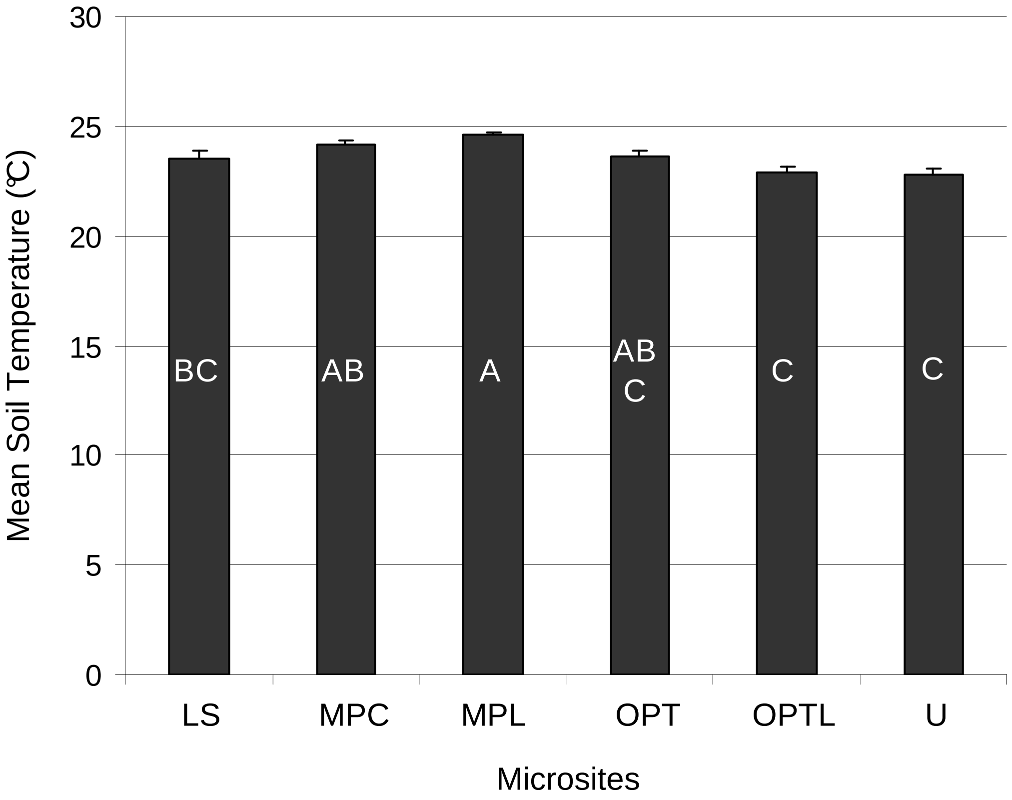


Figure 9. Soil temperature for each microsite created by harvesting machinery. Error bars represent 1 SE. Unique letters indicate significantly different microsites utilizing Tukey’s HSD. LS = 1-pass log skid, MPC = multiple-pass compacted track, MPL = multiple-pass loosened, OPT = 1-pass compacted track, OPTL = 1-pass compacted track with litter, U = undisturbed.

Table 2. Multivariate regression for *Microstegium vimineum* percent cover, mean stem length, mean number of seed heads/stem, and mean number of nodes/stem. Significant values marked with asterisk (*).

Variable	Wilks' Lambda	F	df	*p*
Overall Model	0.261	4.97	12, 90.247	<0.001*
Percent canopy	0.518	7.91	4, 34	<0.001*
Soil temperature	0.580	6.16	4, 34	<0.001*
Soil moisture	0.688	3.85	4,34	0.011*

Thunb. (Caprifoliaceae) (Table 3-8). In undisturbed paired plots not sown with the exotic grass, *M. vimineum* was not a dominant plant (Table 8). While *M. vimineum* was one of the dominant plants in sown plots, species diversity was not correlated with *M. vimineum* percent cover ($r_{34} = 0.20$, $p > 0.05$).

Discussion

Microsites labeled as MPC and MPL were characterized as having the lowest canopy cover and among the highest soil temperatures (Fig. 3, 9). As stated previously, logging machine operators created these microsites through repeated passes with equipment where canopy cover was reduced due to the need for clear operating area and soil temperature was increased as a result of increased exposure to solar radiation. In these microsites with low percent canopy cover, increased soil temperature, and, in the case of MPC, increased soil moisture, *M. vimineum* percent cover was substantially greater than in other microsites due to the favorable growth environment (Table 3-8). In both sown and un-sown plots within MPC and MPL microsites, *M. vimineum* percent cover was at least 40 percent greater than the next most dominant plant species within the set of the 5 most abundant species (Table 4, 5). Also, percent cover of *M. vimineum* was more than 75 and 33 percent greater than the next most dominant species within OPT microsites in sown and un-sown microsites, respectively. It is plausible to attribute the occurrence of increased percent cover of *M. vimineum* to alterations in the above-mentioned environmental variables resulting from the selective harvest activities.

Table 3. Dominance values of the five most dominant species for disturbance category LS (1-pass log skid) plots created by sown and un-sown with *Microstegium vimineum*. Dominance = total area covered per species / total area sampled.

	Dominance
Species	Sown
Liriodendron tulipifera	2.74
Lonicera japonica	9.06
Microstegium vimineum	74.36
Parthenocessus quinquefolia	3.93
Toxicodendron radicans	6.50
	Un-sown
Liriodendron tulipifera	3.42
Lonicera japonica	4.10
Microstegium vimineum	14.02
Parthenocessus quinquefolia	5.30
Toxicodendron radicans	7.35

Table 4. Dominance values of the five most dominant species for disturbance category MPC (multiple-pass compacted, created by repeated passes of a rubber-tired skidder, bulldozer, or both, leaving little or no vegetation or litter) plots sown and un-sown with *Microstegium vimineum*. Dominance = total area covered per species / total area sampled.

	Dominance
Species	Sown
Lespedeza cuneata	6.67
Lonicera japonica	6.03
Microstegium vimineum	97.30
Oxalis stricta	2.54
Toxicodendron radicans	2.86
	Un-sown
Dichanthelium aciculare	2.22
Lonicera japonica	5.24
Microstegium vimineum	70.32
Oxalis stricta	2.06
Toxicodendron radicans	2.86

Table 5. Dominance values of the five most dominant species for disturbance category MPL (multiple-pass loosened, created as the track or tire pushed loose soil up along sides of ruts) plots sown and un-sown with *Microstegium vimineum*. Dominance = total area covered per species / total area sampled.

	Dominance
Species	Sown
Lespedeza cuneata	2.59
Lonicera japonica	9.26
Microstegium vimineum	80.19
Toxicodendron radicans	5.00
Ulmus rubra	2.22
	Un-sown
Carex sp.	2.59
Lespedeza cuneata	3.52
Lonicera japonica	5.00
Microstegium vimineum	72.22
Toxicodendron radicans	3.33

Table 6. Dominance values of the five most dominant species for disturbance category OPT (1-pass compacted track without litter, created by a bulldozer moving through and removing litter in the track marks) plots sown and un-sown with *Microstegium vimineum*. Dominance = total area covered per species / total area sampled.

	Dominance
Species	Sown
Erechtites hieracifolia	2.02
Lonicera japonica	4.65
Microstegium vimineum	87.88
Rubus sp.	2.02
Toxicondendron radicans	1.62
	Un-sown
Liriodendron tulipifera	5.05
Lonicera japonica	4.04
Microstegium vimineum	47.27
Parthenocessus quinquefolia	3.23
Toxicondendron radicans	2.22

Table 7. Dominance values of the five most dominant species for disturbance category OPTL (1-pass compacted track with litter, created by a bulldozer moving through and leaving litter intact in the track marks) plots sown and un-sown with *Microstegium vimineum* . Dominance = total area covered per species / total area sampled.

	Dominance
Species	Sown
Acer rubrum	4.22
Lonicera japonica	11.56
Microstegium vimineum	51.56
Parthenocissus quinquefolia	6.67
Poa sp.	4.89
	Un-sown
Acer rubrum	3.56
Albizia julibrissin	3.11
Lonicera japonica	8.44
Microstegium vimineum	13.11
Parthenocissus quinquefolia	3.33

Table 8. Dominance values of the five most dominant species for disturbance category U (undisturbed, areas where machinery did not disturb the litter or mineral soil) plots sown and un-sown with *Microstegium vimineum*. Dominance = total area covered per species / total area sampled.

	Dominance
Species	Sown
Erechtites hieracifolia	2.22
Lonicera japonica	5.13
Microstegium vimineum	24.27
Parthenocissus quinquefolia	1.54
Toxicodendron radicans	1.37
	Un-sown
Acer rubrum	1.54
Lonicera japonica	5.81
Parthenocissus quinquefolia	1.20
Prunus serotina	1.03
Toxicodendron radicans	3.25

Growth of *M. vimineum* in microsites with decreased percent canopy cover was consistent with the findings of Cole and Weltzin (2005). *M. vimineum* grown under *Asimina triloba* canopy cover had shorter shoot height than *M. vimineum* grown outside canopy cover (Cole and Weltzin, 2005). Also, Barden (1996) observed that as photosynthetically-active photon flux density increased, biomass of potted *M. vimineum* also increased.

Reduced PAR and increased litter depth found in the sown and un-sown, undisturbed plots might provide a strong barrier to *M. vimineum* invasion. Within the un-sown, undisturbed plots, this exotic species did not become a dominant plant (Table 8) and actually did not occur in the un-sown, undisturbed plots at all, perhaps because of the lack of sunlight and the presence of a deep litter layer hindering the emergence of *M. vimineum*. While *M. vimineum* is adapted to varying light conditions, including low light levels (Horton and Neufeld, 1998; Cheplick, 2006), *M. vimineum* experienced reduced growth and reduced dominance in undisturbed plots (Table 8; Fig. 6, 7). In fact, *M. vimineum* was not encountered in unsown, undisturbed plots. Since OPT and OPTL plots received PAR levels similar to undisturbed plots, it appears the addition of soil disturbance may be sufficient to facilitate the growth and dominance of *M. vimineum* in Central Hardwood forests. Increased compaction, increased soil moisture, and decreased litter depth accompany soil disturbance in these microsites.

Much of the focus concerning impacts of haul roads and skid trails has been centered on soil erosion and runoff (e.g. Hartanto et al., 2003; Germain and Munsell, 2005). In addition to impacts on soil erosion and water quality, my results suggest that skid trails and haul roads are associated with key disturbances that may increase the susceptibility of Central Hardwood forests to invasion by *M. vimineum*, and perhaps other exotics. While haul roads and skid trails provide access to forests for management of timber and wildlife, forest protection, and recreation, they can have detrimental effects at local and landscape scales. Careful planning and use of haul road and skid trail networks are clearly important for reducing the surface area of compacted and exposed soil.

Theories forwarded by Kennedy et al. (2002), Naeem et al. (2000), and Thuiller et al. (2006) provide some understanding of what barriers to invasion may exist. However, these theories require the removal of other extrinsic factors, including disturbance. Disturbance is an inevitable occurrence within Central Hardwood forests. Whether these disturbances are human or naturally induced, alterations to physical soil conditions, moisture availability, and light intensity will occur at varying levels and scales. Hypotheses that do not include these extrinsic factors may have limited applicability in situations similar to those presented here. In this study in a Central Hardwood forest, plant diversity was not correlated with *M. vimineum* percent cover. This suggests that in scenarios involving disturbances related to selective harvest techniques, plant diversity does not necessarily limit or facilitate *M. vimineum* dominance.

Future research is needed to further understand how *M. vimineum* spreads and interacts with native species. Spread studies may provide more insight into how various harvesting techniques facilitate the establishment of *M. vimineum* through the creation of suitable habitat and the movement of seed. In addition to information regarding where *M. vimineum* will invade, it is also important to understand how it will interact with regenerating forests after harvest. More information on the impacts of this invasive species on native tree seedlings is necessary to quantify its ecological impacts.

CHAPTER III

INFLUENCE OF LITTER REMOVAL AND MINERAL SOIL DISTURBANCE ON THE SPREAD OF *MICROSTEGIUM VIMINEUM* IN A CENTRAL HARDWOOD FOREST

Abstract

Within Central Hardwood forests, soil and litter disturbance are common and may facilitate exotic plant species invasion into interior portions of the forest. *Microstegium vimineum* is an annual exotic grass that has become common throughout the Southeastern United States. Three replicates of three different soil and litter disturbance treatments, plus a control with no disturbance, were established on the leading edge of *M. vimineum* patches with similar forest canopy and slope in three Central Hardwood forest stands prior to seed fall. At the beginning of the following growing season, each individual *M. vimineum* plant was mapped within the treatment plots. The mean number of *M. vimineum* individuals that established within each treatment did not differ significantly from the control. The distance at which 90 percent of the individuals had spread, and the overall mean distance spread were significantly higher for the litter removal treatment than the control. The farthest individual seedling from the boundary of existing patches in both the litter removal and the mineral soil disturbance and litter removal treatments were higher than the control. The individuals that spread the farthest are of most concern due to the large number of viable seed that a single *M. vimineum* plant can produce. These results suggest that disturbance of the litter layer may increase the spread rate of *M. vimineum* and facilitate its invasion of new habitats, and leaving litter layers intact may slow the spread of *M. vimineum*.

Introduction

Disturbance within forested ecosystems is important in the facilitation of exotic plant species invasion (Elton, 1958; di Castri, 1989; Myers and Bazely, 2003; Lockwood et al., 2007). As a natural process, disturbance alters successional pathways by disrupting the composition, structure, and functionality of ecosystems (Pickett and White, 1985; Barnes et al., 1998). Such changes in composition and functionality can increase the availability of unused resources providing suitable invasion sites for some exotic species, dubbed the fluctuating resource hypothesis (Davis et al., 2000). Human-induced disturbances such as road construction, use, and management can also create invasion sites for exotic plant species. In these situations, the disturbance not only releases suitable habitat, but it provides a corridor for invasion into undisturbed areas (Chapter II; Buckley et al., 2003; Gelbard and Belnap, 2003; Johnston and Johnston, 2004; Lundgren et al., 2004; Parendes and Jones, 2000). In addition to major disturbances related to construction and forest management, recreational activities also result in adequate disturbance intensity to facilitate invasion by exotic plant species (Lloyd et al. 2006). The facilitation of invasion by disturbance can impact not only establishment, but also survival and biomass accumulation of exotic species invading different ecosystems (Domenech and Vila, 2006; Kollmann et al., 2007).

An exotic plant species that has recently received increased attention in the private and public sectors is *Microstegium vimineum* (Trin.) A. Camus

(Poaceae) (Johnson, 1997*b*; Steele et al., 2006). Native to Japan, Korea, and throughout lower mountain regions in Southwestern Asia, *M. vimineum* collections were first made in North America in 1919 near Knoxville, TN (Fairbrothers and Gray, 1972; Osada, 1989; Sur, 1985). Since that time, individuals have spread throughout the eastern United States as far west as Texas and as far north as New York (Hunt and Zaremba, 1992; USDA, 2007).

Microstegium vimineum is an annual C_4 grass most commonly found in areas with moist soils, and is a prolific seeder with high seed viability that may add to its invasive ability (Redman, 1985; Barden, 1987; Williams, 1998; Chapter II). Increased forest canopy cover may limit establishment and growth of *M. vimineum* in Central Hardwood forests. However, under a range of light levels, *M. vimineum* individuals have been shown to acclimate fairly rapidly to shade and accumulate similar amounts of biomass (Winter et al., 1982; Horton and Neufeld, 1998; Cole and Weltzin, 2005; Chapter II). Like many other exotic species responding to natural and human-induced disturbances, *M. vimineum* readily invades disturbed areas (Barden, 1987). This species may be well adapted for further invasion in hardwood forests due to its ability to utilize disturbed areas and considerable phenotypic and its developmental plasticity (Cheplick, 2006).

An understanding of dispersal modes and other mechanisms that facilitate exotic plant species invasion is important for management of these organisms (Davies and Sheley, 2007). In addition to understanding the ecological impacts of *M. vimineum* on herbaceous and woody plants and insect communities (Carroll, 2003; Leicht et al., 2005; Chapter II, IV, V), it is important to be able to identify and evaluate the susceptibility of areas to invasion to increase the efficiency and effectiveness of management techniques, especially in situations of limited managerial resources. Repeated growing season applications of post-emergence herbicides have been shown to significantly decrease *M. vimineum* biomass and seed production compared to a single application (Gover et al., 2003; Judge et al., 2005*a,b*). Targeting areas for control that are most sensitive to invasion as a result of disturbance may limit *M. vimineum* spread and its colonization of new habitats.

Within forests with intact canopies, personal observations suggested that *M. vimineum* had spread rapidly in areas with soil disturbance. It was also observed that in similar areas without soil disturbance, *M. vimineum* displayed reduced spread. In these undisturbed areas, a distinct patch edge was observed. These observations within Central Hardwood forests provided impetus for the hypothesis that litter removal and/or mineral soil disturbance may expedite the spread of *M. vimineum* into areas with relatively intact canopies.

The objectives of this study were to 1) quantify the effects of litter removal and mineral soil disturbance on the spread of *M. vimineum* seedlings within Central Hardwood forests and 2) investigate the hypothesis that disruption of the litter layer and mineral soil facilitates the spread of *M. vimineum* seedlings.

Methods

Spread of *M. vimineum* seedlings was quantified within a manipulative field study conducted at the University of Tennessee Forest Resources Research and Education Center at Oak Ridge, TN (36°00' N, 84°13' W) in the Appalachian Ridge and Valley Physiographic Region. The study area also falls within the Appalachian section of the Central Hardwood forest, which is dominated by the Oak-Hickory forest type (Fralish 2003). Soils are a silty clay loam and classified as ochreptic hapludults (USDA 1981). Mean annual temperature is 15°C and mean annual precipitation is approximately 1500 mm (NCDC 2005).

Three treatments, litter removal, mineral soil disturbance, and mineral soil disturbance and litter removal combined, were assigned at random along with undisturbed controls to 1-m^2 plots. In litter removal plots, all leaf and woody litter was removed by hand. In mineral soil disturbance plots, the soil was disturbed using a sharpshooter shovel, while leaving the litter layer as intact as possible. In the mineral soil disturbance and litter removal combined plots, litter was removed by hand and a sharpshooter shovel was utilized to loosen the soil. In control plots, litter was left intact and the mineral soil was not disturbed. Each treatment and the controls were replicated three times in each of three blocks located in different sites. One block was established as a pilot study in mid-October 2005, and the remaining two were established in mid-October 2006. Implementation of treatments in two consecutive years provided an opportunity to catch potential year-to-year differences in dispersal and emergence patterns. The 1-m^2 quadrat, used to delineate the treatment area, was positioned along the edge of an established *M. vimineum* patch. All patches were located along road edges and had defined edges where *M. vimineum* had not spread. Within all treatments, including the control, any stray *M. vimineum* individuals that occurred within the frame during the treatment process were removed and all other living vegetation was not removed.

Forest canopy cover was measured using a concave spherical densiometer (Forest Densiometers, Bartlesville, OK) during the spring of the growing season following the establishment of the treatments. Slope and aspect were measured in second year of the study for blocks 1 and 2. Slope was measured using an Abney level in the center of the plot and along the two parallel sides along the plot axis perpendicular to the leading edge of the existing *M. vimineum* patch.

During the following growing season, on 29 March 2006 and 5, 9, and 10 April 2007, the X and Y coordinates of all *M. vimineum* individuals were recorded within each quadrat to the nearest millimeter using two meter sticks. The distance from the original patch edge in which 90 percent of the individuals occurred within each plot was calculated. Differences in mean distance of spread and the distance capturing 90 percent of individuals between treatments were analyzed using an analysis of variance (ANOVA).

Also, each plot was divided into four 25 cm zones and the number of individuals per zone was calculated. An ANOVA was utilized to identify if differences across treatments occurred in the number of individuals within each zone. Differences in percent canopy cover between blocks and treatments were identified with a nested ANOVA. A square root transformation was applied to data that did not meet the assumptions of normality. Tukey's HSD was used for post-hoc multiple comparison for percent canopy cover and percent slope. One-tailed Dunnett's post-hoc tests were utilized to test whether distances and counts in treatments were greater than the control. Linear regression was used to test the relationship between slope and the distance of the farthest individual in the plot. All analyses were performed with $\alpha = 0.05$ in SAS (SAS Institute Inc., Cary, NC, Version 9.1.3).

Results

Percent forest canopy cover and percent slope did not significantly differ among treatments (Table 9). Within each treatment, there was large variability in the number of individuals and the distance of the farthest individual (Fig. 10-13). No substantial differences in patterns between years were detected. It is possible that spread of *M. vimineum* could have occurred past the 1-m^2 plot. However, for most of the replicates, the density of *M. vimineum* individuals decreases with increased distance from the patch edge (Fig. 10-13). No *M. vimineum* individuals emerged in one control plot (Block 3, Replicate 1) (Fig. 10). The number of *M. vimineum* individuals within each treatment required a square root transformation to meet the assumption of

Table 9. Mean percent forest canopy cover (SE) and percent slope (SE) for differing litter and mineral soil disturbances.

Treatment		Percent Canopy Cover	Percent Slope
Control		89.63 (0.94)	-8.15 (5.88)
Mineral soil disturbance		91.54 (0.54)	-17.10 (4.36)
Litter removal		90.78 (1.02)	-3.78 (2.41)
Mineral soil disturbance and litter removal		91.39 (0.57)	-1.08 (3.47)
	F_{df}	$1.51_{3,30}$	$2.98_{3,19}$
	p	0.233	0.06

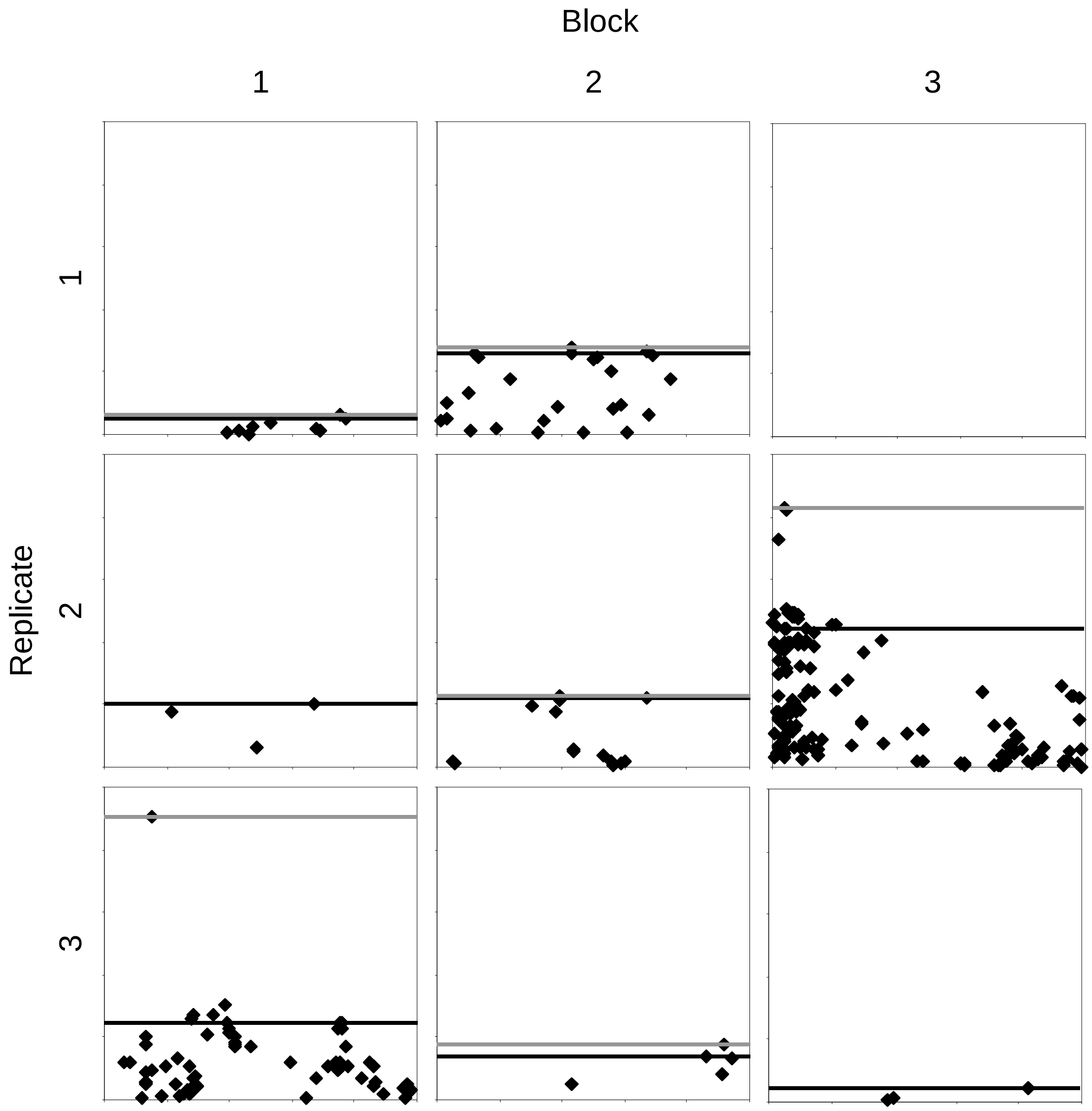


Figure 10. Plot maps of *Microstegium vimineum* individual locations within 1-m^2 control plots. Black line indicates the distance at which 90 percent of *M. vimineum* seedlings are captured. Gray line indicates the distance of the farthest *M. vimineum* individual. Note: Block 3, replicate 1 had zero *M. vimineum* individuals. The bottom line of each plot map corresponds to the edge of the existing *M. vimineum* patch during treatment implementation.

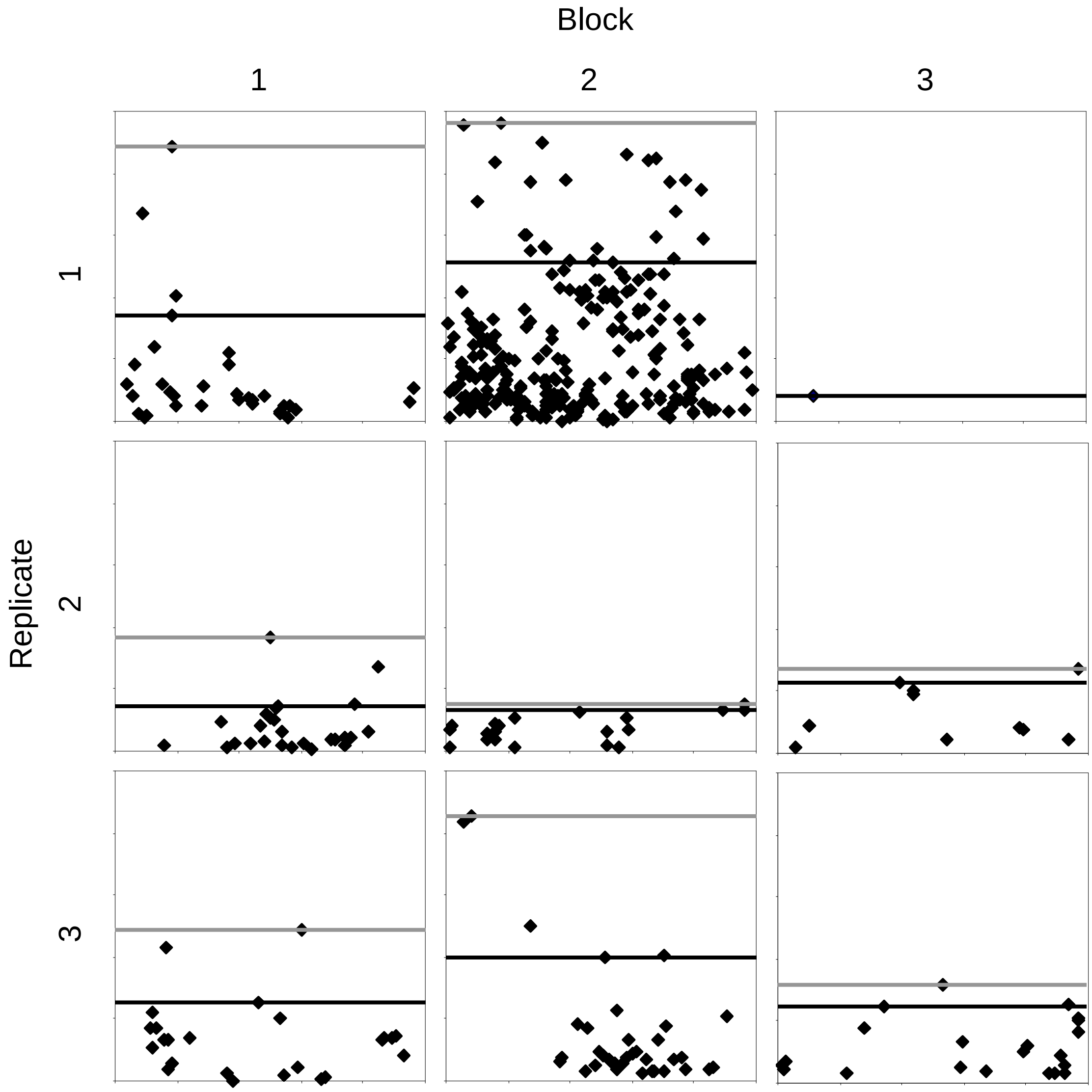


Figure 11. Plot maps of *Microstegium vimineum* individual locations within 1-m^2 replicates receiving the mineral soil disturbance treatment. Black line indicates the distance at which 90 percent of *M. vimineum* seedlings are captured. Gray line indicates the distance of the farthest *M. vimineum* individual. Note: The bottom line of each plot map corresponds to the edge of the existing *M. vimineum* patch during treatment implementation.

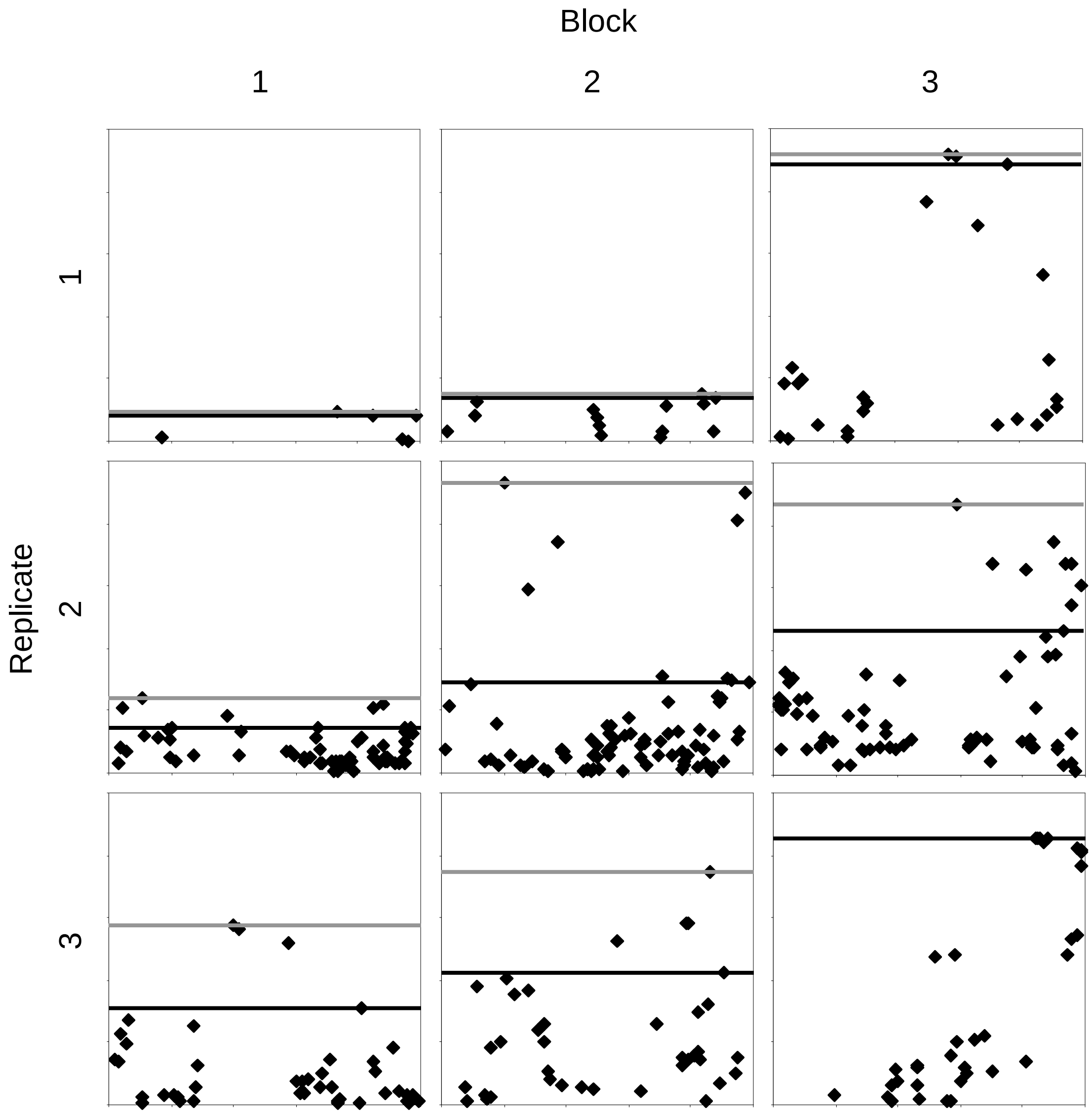


Figure 12. Plot maps of *Microstegium vimineum* individual locations within 1-m^2 replicates receiving the litter removal treatment. Black line indicates the distance at which 90 percent of *M. vimineum* seedlings are captured. Gray line indicates the distance of the farthest *M. vimineum* individual. Note: The bottom line of each plot map corresponds to the edge of the existing *M. vimineum* patch during treatment implementation.

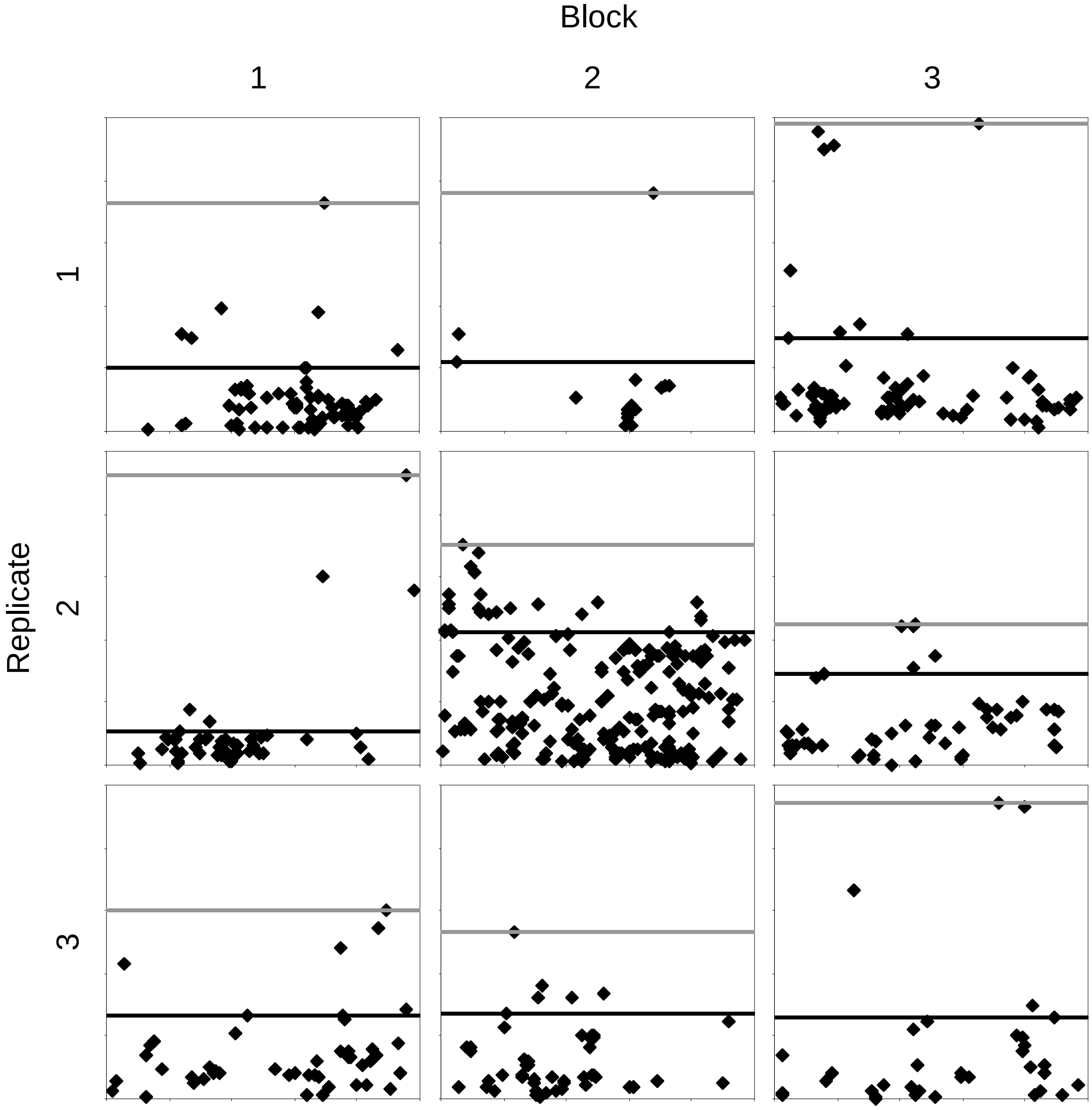


Figure 13. Plot maps of *Microstegium vimineum* individual locations within 1-m^2 replicates receiving the mineral soil disturbance and litter removal treatment. Black line indicates the distance at which 90 percent of *M. vimineum* seedlings are captured. Gray line indicates the distance of the farthest *M. vimineum* individual. Note: The bottom line of each plot map corresponds to the edge of the existing *M. vimineum* patch during treatment implementation.

normality and there was not a significant difference between any of the treatments and the control ($F_{3,36}$ = 1.57, p = 0.216) (Fig. 14). In addition to this, the mean number of *M. vimineum* individuals within each 25 cm zone did not differ among treatments (Table 10).

The distance at which 90 percent of *M. vimineum* individuals were captured did not differ significantly among treatments according to the overall ANOVA ($F_{3,36}$ = 2.37, p = 0.090). However, Dunnett's test indicated the distant at which 90 percent of individuals were captured in the litter removal treatment was significantly greater than in the control (Fig. 15). Mean spread distance in the litter removal treatment was significantly greater than in the control according to Dunnett's test (Fig. 16). However, the overall ANOVA for the mean distance spread was not significant ($F_{3,36}$ = 1.75, p = 0.178). Distance of the farthest *M. vimineum* individual was significantly greater in the litter removal and mineral soil disturbance and litter removal combined treatments than in the control ($F_{3,36}$ = 3.68, p = 0.023) (Fig. 17). A linear relationship did not exist between percent slope and distance spread by the farthest *M. vimineum* individual (R^2 = 0.006, $F_{1,22}$ = 0.13, p = 0.726).

Discussion

The number of *M. vimineum* seedlings that occurred within the plot was not related to the treatment applied or the slope of the plots (Fig. 14, Table 10). However, the distance *M. vimineum* seedlings spread into the plot was influenced by the disturbance applied to the plot (Fig 15-17). Mean

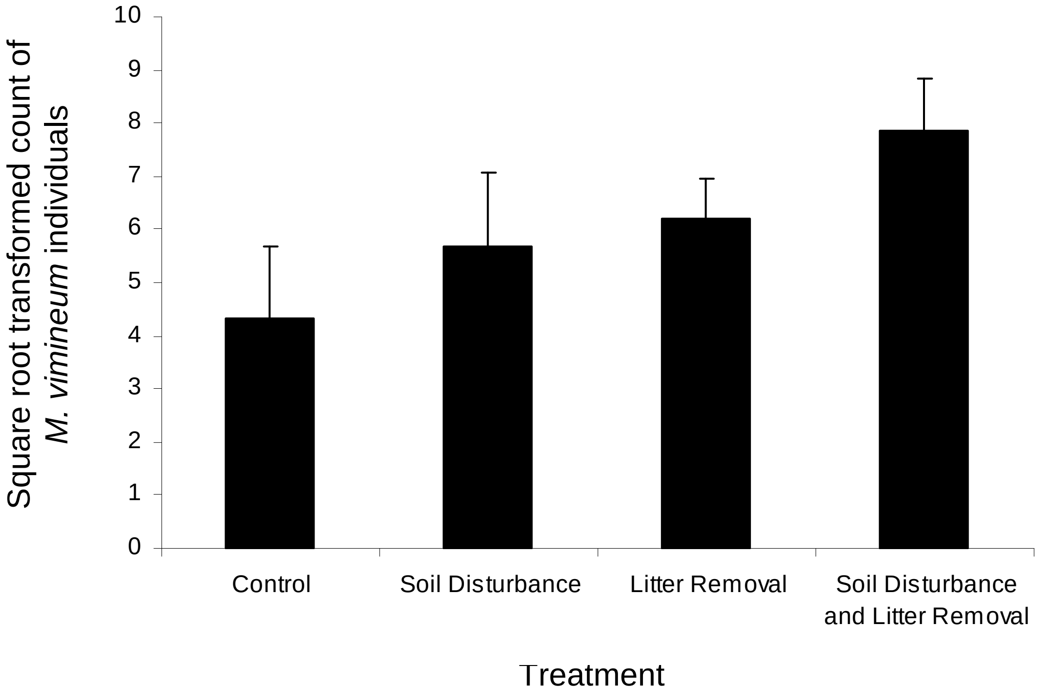


Figure 14. Square root transformed mean (SE) count of *Microstegium vimineum* individuals across treatments.

Table 10. Mean count of *Microstegium vimineum* seedlings (SE) in 25 cm zones by treatment. Note: Zone 1 corresponds to 0.0-25.0 cm from the *M. vimineum* edge present during treatment implementation; Zone 2 corresponds to 25.1-50.0 cm from the edge; Zone 3 corresponds to 50.1-75.0 cm from the edge; and Zone 4 corresponds to 75.1-100.0 cm from edge.

Zone	Treatment	Count	$F_{3,30}$	*p*
1			0.92	0.441
	Control	25.89 (12.93)		
	Soil Disturbance	35.67 (16.35)		
	Litter Removal	35.56 (8.35)		
	Soil Disturbance Litter Removal	55.44 (11.79)		
2			0.31	0.819
	Control	6.56 (5.35)		
	Soil Disturbance	8.44 (6.83)		
	Litter Removal	3.56 (1.36)		
	Soil Disturbance Litter Removal	11.00 (7.29)		
3			0.93	0.439
	Control	0.11 (0.11)		
	Soil Disturbance	2.11 (1.65)		
	Litter Removal	2.22 (0.76)		
	Soil Disturbance Litter Removal	2.00 (1.03)		
4			0.71	0.551
	Control	0.33 (0.24)		
	Soil Disturbance	1.56 (1.20)		
	Litter Removal	1.89 (1.02)		
	Soil Disturbance Litter Removal	0.89 (0.45)		

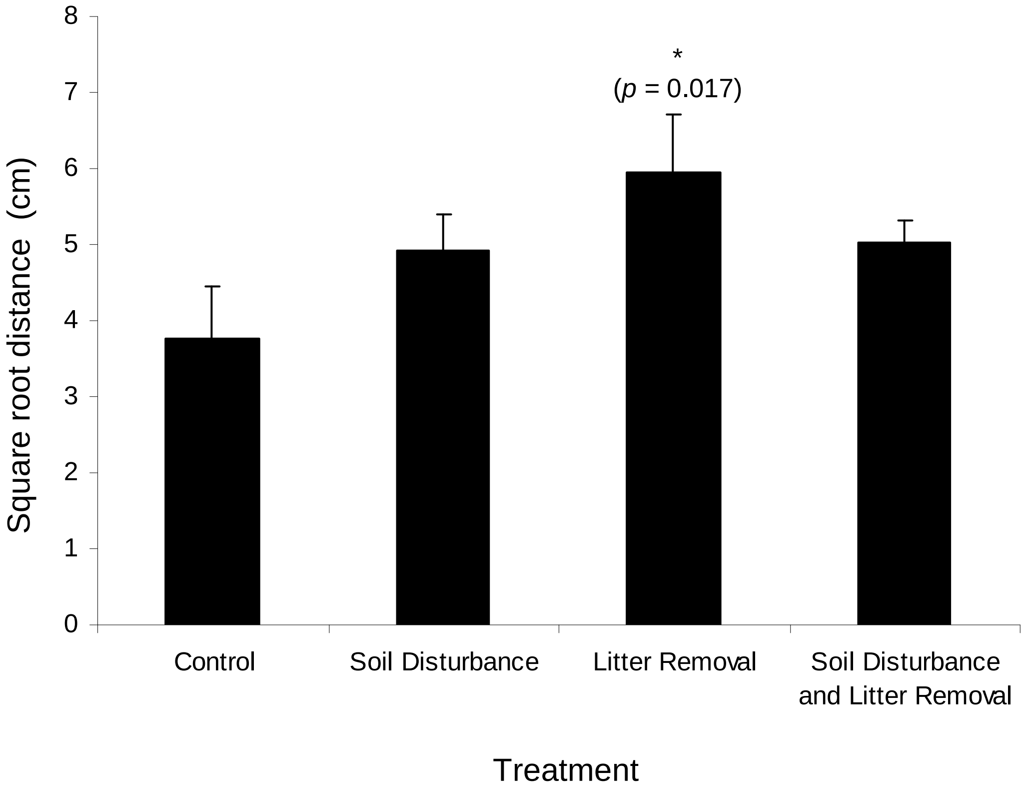


Figure 15. Mean (SE) distance at which 90 percent of *Microstegium vimineum* seedlings are captured. Asterisk (*) indicates significant differences between the treatment and the Control from Dunnet's post-hoc test (with *p*-value). Note: Data required square root transformation to meet assumption of normality.

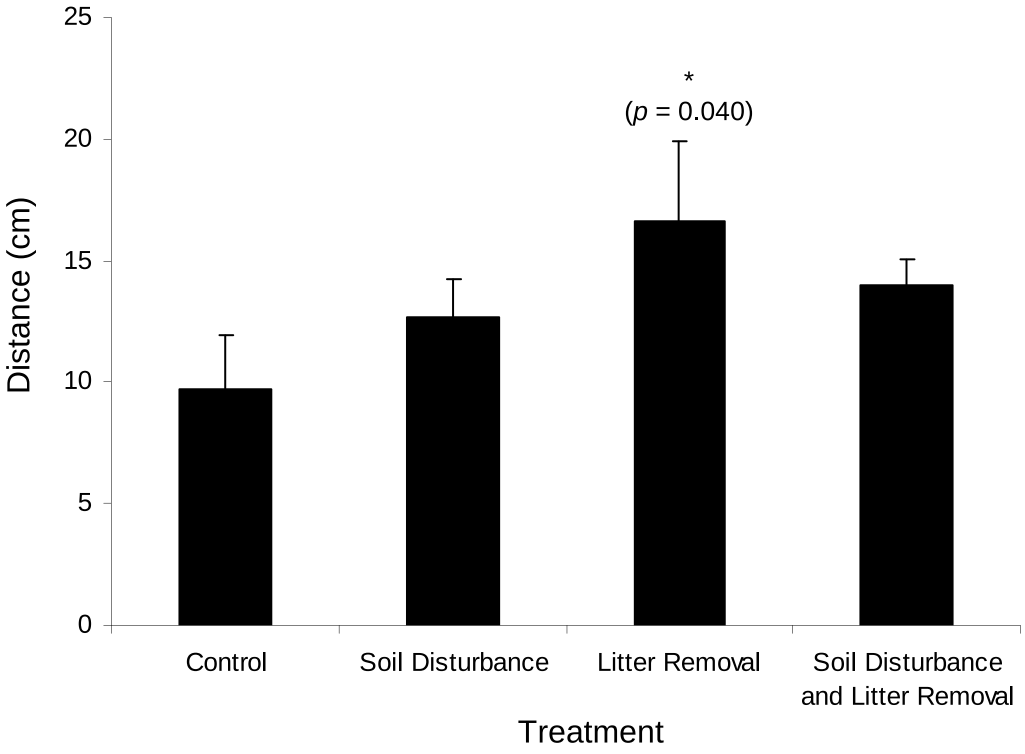


Figure 16. Mean (SE) spread distance for *Microstegium vimineum* seedlings. Asterisk (*) indicates significant differences between the treatment and the Control using Dunnet’s post-hoc test.

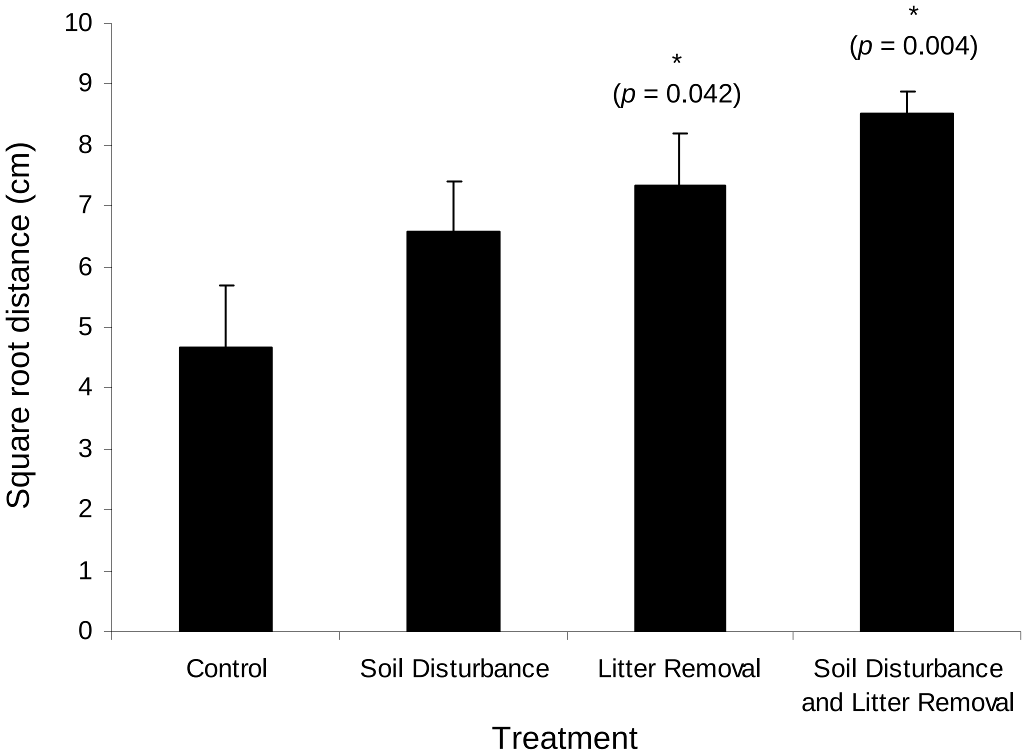


Figure 17. Mean (SE) distance for the farthest *Microstegium vimineum* individual occurring from the leading edge. Asterisk (*) indicates significant differences between the treatment and the control from Dunnet's post-hoc test. Note: Data required square root transformation to meet assumption of normality.

distances of seedlings from the patch edge of the source populations were greater in the litter removal plots than in the controls. It has been shown that seedbed texture, including litter, affects the dispersal of seeds, thereby altering forest seed bank composition (Ghorbani et al., 2006). Greater spread in the litter removal treatment may have been due to the lack of litter, and also the lack of the roughened soil surface that resulted from the mineral soil disturbance treatment. The relatively smooth surface allowed for more seed to move further, increasing the mean distance spread (Fig. 16). It is reasonable to assume *M. vimineum* seedling numbers and distribution are a function of both dispersal distance and germination. However, the intrinsically high germination rates in this species and greater spread in the litter removal treatment suggests that spread of *M. vimineum* into newly disturbed habitat, within a closed canopy forest, may be more a function of where seed lands and the rate at which it spreads from the source populations than a function of germination, which is influenced by external factors imposed by the environment. In addition, the similarity and relative closure of the forest canopy, approximately 90 percent canopy across all treatments provides further evidence for the overall invasiveness of *M. vimineum* in hardwood forests, and the beneficial effects of soil and litter disturbance on spread.

It can be argued that the *M. vimineum* seeds that germinate the farthest from the patch edge of existing stands are of the greatest interest. A single *M. vimineum* individual can produce up to approximately 77 seeds with 80 to 90 percent viability (Williams, 1998; Chapter II). The extension of *M.*

vimineum patches due to spread resulting from disturbance in this study ranged from 54 to 72 cm for litter removal and soil disturbance combined with litter removal treatments, respectively (Fig. 17). Spread in treated plots was 2.5-3 times greater than the 22 cm spread observed in the control plots (Fig. 17). Some exotic and invasive plant species require a disturbance within the natural system to establish by seed, even when dispersal barriers are experimentally removed (Jesson et al., 2000). While *M. vimineum* does not seem to be such a species, as suggested by its ability to disperse and establish individuals in the undisturbed control plots, these results suggest that litter and soil disturbance can facilitate the movement of seed and the establishment of distant individuals. Seed movement has been shown to be the limiting factor in establishment and spread of other exotic plant species (Kollmann et al., 2007), and this appears to also be the primary case with *M. vimineum*.

While this study was not designed to reveal overall success of an individual or population of *M. vimineum* after establishment (Chapter II), it does provide some understanding as to what forested areas may be more susceptible to invasion as a function of proximity to entrenched populations and disturbance regimes. In areas where *M. vimineum* has become established, limiting disturbances that disrupt or destroy litter may, in turn, slow the spread of this species into more interior forest areas. Conversely, increases in soil and litter disturbance may increase the rate at which established populations of *M. vimineum* spread into the interior of a forest.

CHAPTER IV

COMPETITIVE INTERACTIONS BETWEEN THE EXOTIC GRASS *MICROSTEGIUM VIMINEUM* AND NATIVE HARDWOOD SEEDLINGS

Abstract

Competition between plant species plays an important role in forest succession and composition. The addition of an exotic species, such as the annual grass *Microstegium vimineum*, may alter the composition of future forests through inhibition of growth and recruitment of seedlings into larger size classes. The influence of *M. vimineum* on biomass accumulation in *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus rubra* seedlings was quantified in a planting bed study under 50 percent shade. There was a reduction in *A. rubrum* and *L. tulipifera* leaf area as a result of soil moisture competition with *M. vimineum.* There was also a reduction in *L. tulipifera* specific leaf weight, which suggests competition for soil nutrients. *Quercus rubra* did not display any differences in leaf characteristics as a result of *M. vimineum* competition. While *M. vimineum* competition did reduce growth in these species, seedling mortality was very low and not related to the presence of *M. vimineum*. None of the tree species imposed measurable competitive impacts on above-ground weight, seed mass, or seed count for *M. vimineum*. The height of *M. vimineum* was significantly related to tree seedling stem lengths. A likely explanation for this relationship is that neighboring seedlings were providing vertical structure for the stems of this grass, which are often recumbent. As a result of reductions in the growth of *A. rubrum* and *L. tulipifera*, competitive impacts imposed by *M. vimineum* may alter the rate at which these species are recruited into larger size classes. This alteration to recruitment may

change future forest composition, thereby having ecological and economic consequences.

Introduction

Microstegium vimineum (Trin.) A. Camus (Poaceae) is a C_4 grass introduced to North America from Southeastern Asia (Fairbrothers and Gray, 1972; Osada, 1989; Sur, 1985). It is found throughout the Eastern United States from Florida to Massachusetts and as far west as Texas (Fairbrothers and Gray, 1972; Hunt and Zaremba, 1992; USDA, 2007). *Microstegium vimineum* is able to acclimate to varying levels of available light (Horton and Neufeld, 1998). This physiological plasticity may contribute to the ability of this species to spread into disturbed forests, which it readily invades (Barden, 1987; Cheplick, 2006).

Within the Central Hardwood forests of North America, *Acer rubrum* L. (Aceraceae), *Liriodendron tulipifera* L. (Magnoliaceae), and *Quercus rubra* L. (Fagaceae) are important components of dominant and codominant forest crown classes (Beckage and Clark, 2003; Schmidt and McWilliams, 2003). *Acer rubrum* is a shade-tolerant tree species common in Oak-Hickory forests within the Central Hardwood region (Eyre, 1980). While *A. rubrum* can survive on a wide range of sites, it performs best on moderately well-drained, moist sites (Walters and Yawney, 1990). Also, in stands where historical fire disturbance is excluded, *A. rubrum* often increases in abundance to become a dominant species (Albrecht and McCarthy, 2006; Blankenship and Arthur, 2006).

Liriodendron tulipifera is a shade-intolerant species associated with Oak-Hickory forests in the Central Hardwood region (Eyre, 1980). Due to its ability to rapidly colonize disturbed sites through seed dispersal and sprouting, *L. tulipifera* is often labeled as a pioneer species (Beck, 1990). Its pioneering ability is also evident in the rapid growth rates of *L. tulipifera* seedlings, which are much higher than those of *A. rubrum* and *Q. rubra* (Beckage and Clark, 2003). Following disturbance, copious seed production and ease of seed dispersal aid in the colonization of sites by *L. tulipifera* (Bonner and Russell, 1974; Clark et al., 1998).

As a species with intermediate shade-tolerance, *Q. rubra* is more tolerant of shade than *L. tulipifera*, but less tolerant than *A. rubra* (Beck, 1990; Sander, 1990; Walters and Yawney, 1990). In a recent study, Beckage and Clark (2003) found that *Q*. *rubra* seedlings out survived *A. rubrum* and *L. tulipifera* seedlings in a range of canopy and understory treatments. Following initially high soil moisture requirements for seed germination and seedling establishment, *Q. rubra* can withstand substantial drought conditions (Sander, 1990; Pritchard, 1991; Tilki and Alptekin, 2006).

Although the ability of *M. vimineum* to establish and spread across landscapes is well known, information on competitive effects of this species in relation to hardwood trees is primarily anecdotal. However, in a recent field study designed by Oswalt et al. (2004) to examine the performance of planted oak seedlings in response to different overstory treatments, possible impacts of *M. vimineum* on *Q. rubra* seedlings were documented. Height growth of *Q.*

rubra decreased as *M. vimineum* biomass increased (Oswalt et al., 2004). Also, native hardwood seedling recruitment may be reduced by *M. vimineum* in Central Hardwood forests because of reductions in germination success of hardwood tree seeds sown in patches of *M. vimineum* (Cole, 2006).

The responses of different species to imposed competitive interactions vary depending on the evolved growth strategy for each species (Harper, 1977; Tilman 1988; Grime, 2001). Those adapted responses will also vary depending on the competing neighbor and the limiting resource (Reynolds, 1999; van Andel, 2005). Interspecific competition between trees and other species influences future forest composition through the limitation of vertical growth and mortality (Barnes et al., 1998; Grime, 2001; Husheer et al. 2006; Royo and Carson, 2006). Competitive interference, where a species alters the accumulation of biomass of another species by competing for resources equally available to both, can change tree species replacement and seedling recruitment (Harper, 1977; Barnes et al., 1998). While interactions in the form of competition or facilitation are a natural component of ecological succession, the addition of exotic competitors may shift natural succession toward an undesired forest composition (Berkowitz et al., 1995; van Andel, 2005; Vidra et al., 2006).

Competitive ability and effects of *M. vimineum* may vary depending on the strategy of a given competitor and the environment. Under ambient sunlight, *M. vimineum* has been shown to effectively out compete two other grasses, *Lolium perenne* ssp. *multiflorum* (Lam.) Husnot, an aggressive annual, and *Muhlenbergia mexicana* (L.) Trin., a C_4 perennial. Under shade, however, the competitive ability of *M. vimineum* did not differ from the other grasses in the experiment (Leicht et al., 2005). It is evident that the reduced competitive ability in shade (at 9% full sunlight) presented by Leicht et al. (2005) is due to the greatly reduced growth of *M. vimineum* in low light conditions in field studies (Chapter II).

To my knowledge, no experiments have been designed or conducted to establish competitive effects of *M. vimineum* on native tree seedling growth and survival. Likewise, no studies have established competitive effects of native tree seedlings on *M. vimineum*. Quantifying the competitive effects of native tree seedlings on *M. vimineum* may provide further understanding as to where this exotic grass is limited in spread and establishment, and possibly what native species hinder its spread. Competition between *M. vimineum* and native hardwood tree seedlings is of concern because of the potential for change in forest composition over time due to reductions in the recruitment of seedlings into larger size classes.

The objectives of this study were to 1) quantify the competitive effects of *M. vimineum* on the seedling growth of three native Central hardwood species of differing life history strategies, 2) identify potential competitive effects of the hardwood seedlings on *M. vimineum* growth, and 3) to test the hypothesis that hardwood tree seedlings of species with differing growth strategies and life histories will respond differently to exotic species competition.

Methods

A randomized complete block design was utilized within planting beds established at the University of Tennessee Forest Resources Research and Education Center at Oak Ridge, TN (36°00' N, 84°13' W). This site is located in the Appalachian Ridge and Valley Physiographic Region. While the location of the study site is an open field, it is within the Appalachian section of the Central Hardwood forest, which is dominated by the Oak-Hickory forest type (Fralish, 2003). Soils are a silty clay loam and classified as ochreptic hapludults (USDA, 1981). Mean annual temperature is 15° C and mean annual precipitation is approximately 1500 mm (NCDC, 2005).

Seed for *M. vimineum* was collected 20 October 2005 from existing populations at the University of Tennessee Forest Resources Research and Education Center at Oak Ridge, TN. *Microstegium vimineum* was dried at 70° C for 24 hours and seeds were collected from dried material with an aspirator. *Quercus rubra* acorns were collected from a single maternal seed source at the Cherokee National Forest Watauga Northern Red Oak Genetic Resource Area on 8 October 2005. Acorns were graded by size and only 2 cm diameter acorns were selected for planting to minimize variation in stored reserves at the outset. Oak seedling size is known to have a positive correlation with acorn size (Aizen and Woodcock, 1996; Kormanik et al. 1998). *Liriodendron tulipifera* seeds were collected from a seed orchard near Knoxville, TN, in 2004. *Acer rubrum* seeds were purchased from Sheffield’s

Seed Co., Inc. (Locke, NY) with a known collection location of Madison County, TN, in 2005.

Microstegium vimineum, *Q. rubra*, and *L. tulipifera* seed were cold stratified in wet sand at 4℃ for 3 months. *Acer rubrum* seeds were soaked for 24 hours and cold stratified in wet sand at 4℃ for 1 month. *Acer rubrum*, *L. tulipifera*, and *Q. rubra* seeds were sown in vermiculite for germination on 1 and 2 March 2006. All tree seedlings were transplanted to the study site on 7 April 2006 with 108 individuals of each species transplanted in each shade house. *Microstegium vimineum* seed was sown directly on the field plots on 7 April 2006, but due to low germination rates it was re-sown on 5 May 2006 after the shade houses were erected, as described below. Both sowing instances were applied at a rate of 150 seeds per plot. Densities of *M. vimineum* were thinned on 24 May 2006 to 60 individuals per plot. Plots were weeded on a 2-4 week cycle to minimize the influence of non-target species.

Planting beds were prepared with the application of glyphosate herbicide on 1 February 2006 and tilled with a tractor-mounted roto-tiller on 1 March 2006. Three 16.2 m X 4.2 shade houses were constructed within the beds using 50% shade cloth (Gempler's, Janesville WI). Complimentary, unshaded plots were initially set up for this experiment, but not used due to the failure of *M. vimineum* seed to germinate. Plots within each shade house were 60 cm X 60 cm, with a 60 cm buffer between each plot. Species mixtures were randomly placed within each shade house. Due to substantial differences between *M. vimineum* individuals and hardwood seedlings in leaf area per individual, 10 *M. vimineum* individuals were considered equal to one hardwood seedling. Species mixtures for a single tree species were replicated three times within each shade house and consisted of six trees with no *M. vimineum*, six trees with 60 *M. vimineum*, and no trees with 60 *M. vimineum*.

Relative differences in soil moisture between plots were measured using a Trase Time Domain Reflectometry (TDR) probe (Soilmoisture Corp., Santa Barbara, CA) with 15 cm waveguides on 20 September 2006. The date for soil moisture measurement was selected during a dry period. Maximum differences in soil moisture between treatments, and perhaps maximum intensity of competition for soil moisture, are most likely to occur during periods of low rainfall. Photosynthetically active radiation (PAR) was measured at 15 cm, 50 cm, and 1 m above the soil surface at the center of each plot using an AccuPAR Linear Ceptometer (Decagon Devices Inc., Pullman, WA) on 20 September 2006. An identical ceptometer was placed in close proximity to the shade houses in full sun, and measured PAR at an interval of 30 seconds. These reference PAR measurements taken in full sun were used to calculate percent full PAR measured within the shade houses. PAR measurements were taken during a two-hour time frame bracketing solar noon to examine any relative differences in PAR between plots.

All tree individuals, as well as *M. vimineum*, were harvested on 2-4 October 2006 and stored in sealed plastic bags at 4℃ until processed. Harvesting was done before tree seedling leaf fall and *M. vimineum* seed maturation and whole plant senescence. Tree seedlings were harvested with a sharpshooter shovel, removing ample soil to harvest as much of the root systems as possible. Stem length was measured to the nearest millimeter and leaf area was measured using a LI-3100 Area Meter (LI-COR Biosystems, Lincoln, NE) for all tree seedlings. Roots were separated from above-ground structures and washed to remove soil. All above- and below-ground structures were dried at 55℃ to a constant weight. Above- and below-ground biomass values were measured and specific leaf weight and root:shoot ratio were calculated.

Microstegium vimineum was clipped at the soil surface using grass shears. The mean height of *M. vimineum* for each plot was calculated from four equally spaced measurement points within each plot immediately prior to harvest. Mean *M. vimineum* height was only collected for two planting bed blocks as one block was inadvertently harvested before this variable was quantified. Above-ground *M. vimineum* structures were dried at 55°C to a constant weight. Seed was removed and collected through shaking and vigorous agitation of sample bags for 60 seconds and the use of a large paper funnel. *M. vimineum* seed was passed through a 1680 micron sieve in an effort to remove all other *M. vimineum* structures. Above-ground biomass and seed weight were measured. Seed count was estimated for each plot by calculating a mean seed weight for random sub-samples of seeds.

Data that did not meet the assumption of normality were transformed using an arcsine square root transformation for proportional data and $\log_{10}$ transformation for continuous data. A two factor analysis of variance

(ANOVA) was used to identify differences in PAR and soil moisture by presence or absence of *M. vimineum* and tree seedling species. A single factor (ANOVA), with shade houses as blocks, was used to identify differences in tree seedling and *M. vimineum* growth variables between treatments. For all ANOVAs, Tukey's HSD was used as a post-hoc test. A log likelihood ratio G-test (Sokal and Rohlf, 1995) was used to test the likelihood that seedling mortality was independent of treatment. All analyses were performed with $\alpha = 0.05$ in SAS (SAS Institute Inc., Cary, NC, Version 9.1.3).

Results

The arcsine square root transformed percent PAR was not significantly different between plots with and without *M. vimineum* or different tree species at any of the three sampling heights of 15 cm, 50 cm, and 1 m (Table 11). The arcsine square root percent volumetric soil moisture was not significantly different between plots with different tree species, but was significantly lower in the treatments with *M. vimineum* than without *M. vimineum*; 0.502 with *M. vimineum* and 0.539 without *M. vimineum* ($F_{1,48} = 7.24$, $p < 0.01$), 23.2 percent and 26.4 percent, respectively, when back-transformed.

It is expected that many of the leaf and above ground growth variables were correlated as most growth is interconnected to the growth of other structures. Although these variables were correlated, individual analyses were performed for each variable in an effort to identify possible mechanisms when statistical differences were indicated.

Table 11. Two-factor analysis of variance of arcsine square root transformed photosynthetically active radiation at three heights in mixtures of *Acer rubrum*, *Liriodendron tulipifera*, *Quercus rubra*, and *Microstegium vimineum (Mv)*.

Height		DF	Mean square	F	*p*
15 cm		5	0.0147	1.58	0.185
	Tree Species	2	0.0100	1.08	0.348
	Mv presence	1	0.0050	0.54	0.465
	Tree Species**Mv*	2	0.0228	2.46	0.097
	Error	45	0.0093		
50 cm		5	0.0209	0.31	0.906
	Tree Species	2	0.0196	0.29	0.750
	Mv presence	1	0.0007	0.01	0.922
	Tree Species**Mv*	2	0.0323	0.48	0.624
	Error	48	0.0679		
1 m		5	0.0014	0.53	0.755
	Tree Species	2	0.0002	0.07	0.929
	Mv presence	1	0.0001	0.05	0.828
	Tree Species**Mv*	2	0.0034	1.22	0.304
	Error	47	0.0027		

A total of 6 *A. rubrum*, 9 *L. tulipifera*, and 6 *Q. rubra* seedlings died out of the 324 individuals of each species planted (Table 12). For each species, mortality was statistically independent of the presence of *M. vimineum* (Table 12). For *A. rubrum*, there were significant differences between plots with and without *M. vimineum* in seedling leaf weight, shoot weight, root weight, total seedling weight, number of leaves per seedling, leaf area, and stem length (Table 13). In all cases of significant differences for *A. rubrum*, values for plots with *M. vimineum* were less than for plots without *M. vimineum* (Table 13).

For *L. tulipifera*, there were significant differences between plots with and without *M. vimineum* in seedling leaf weight, stem weight, shoot weight, root weight, total seedling weight, number of leaves per seedling, and specific leaf weight (Table 14). As with *A. rubrum*, in all cases of significant differences for *L. tulipifera*, values for plots with *M. vimineum* were less than for plots without *M. vimineum* (Table 14). While differences in leaf area were not statistically significant, plots without *M. vimineum* had a higher mean leaf area than plots with *M. vimineum*.

For *Q. rubra*, there were significant differences between plots with and without *M. vimineum* only in seedling stem weight and shoot weight (Table 15). As with *A. rubrum* and *L. tulipifera*, in all cases of significant differences for *Q. rubrum*, values for plots with *M. vimineum* were less than for plots without *M. vimineum* (Table 15). Insect herbivory of *Q. rubra* was noted

Table 12. Log likelihood ratio G-test of tree seedling mortality in treatments with and without *Microstegium vimineum*.

	Mortality (Survival) Count			
Species	With	Without	G_1	p
Acer rubrum	4 (50)	2 (52)	0.177	>0.05
Liriodendron tulipifera	4 (50)	5 (49)	0.489	>0.05
Quercus rubra	3 (51)	3 (51)	0.177	>0.05

Table 13. Single factor ANOVA results for *Acer rubrum* seedlings in plots with and without *Microstegium vimineum* (SE). Asterisks (*) signify significant differences.

	M. vimineum presence			
Variable	With	Without	$F_{1,14}$	*p*
Leaf weight (g)	0.720 (0.224)	2.477 (0.434)	12.78	0.003*
Stem weight (g)	0.637 (0.283)	1.510 (0.329)	3.82	0.071
Shoot weight (g)	1.358 (0.507)	3.987 (0.753)	8.08	0.013*
Root weight (g)	0.108 (0.163)	0.521 (0.101)	12.06	0.004*
Total weight (g)	2.474 (1.004)	6.003 (1.041)	5.62	0.033*
Root:Shoot ratio	-0.019 (0.096)	-0.035 (0.101)	0.09	0.769
Leaf count	0.991 (0.054)	1.168 (0.107)	8.42	0.012*
Leaf area (cm^2)	131.108 (39.380)	466.918 (81.974)	13.46	0.003*
Mean leaf size (cm^2)	8.086 (2.033)	12.938 (1.751)	3.60	0.079
Stem length (cm)	21.187 (2.514)	35.971 (4.250)	8.80	0.010*
Specific leaf weight (mg/cm^2)	5.401 (0.256)	5.277 (0.112)	0.22	0.648

Note: Variables Root weight, Root:Shoot ratio, and Leaf count required Log_{10} transformation to meet assumptions of normality. Negative values are a result of the transformations applied to the data.

Table 14. Single factor ANOVA results for *Liriodendron tulipifera* seedlings in plots with and without *Microstegium vimineum*. Asterisks (*) signify significant differences

	M. vimineum presence			
Variable	With	Without	$F_{1,14}$	*p*
Leaf weight (g)	0.064 (0.086)	0.427 (0.098)	8.44	0.012*
Stem weight (g)	-0.116 (0.089)	0.231 (0.097)	7.39	0.017*
Shoot weight (g)	0.288 (0.085)	0.645 (0.094)	8.66	0.011*
Root weight (g)	0.188 (0.124)	0.521 (0.084)	8.13	0.013*
Total weight (g)	0.560 (0.098)	0.890 (0.085)	7.05	0.019*
Root:Shoot ratio	0.449 (0.057)	0.486 (0.056)	0.29	0.602
Leaf count	0.996 (0.058)	1.157 (0.119)	5.99	0.028*
Leaf area (cm^2)	2.342 (0.107)	2.631 (0.147)	4.58	0.050
Mean leaf size (cm^2)	85.280 (15.313)	93.430 (9.735)	0.36	0.560
Stem length (cm)	40.832 (7.435)	46.573 (8.518)	0.43	0.524
Specific leaf weight (mg/cm^2)	3.316 (0.199)	4.069 (0.136)	8.91	<0.001*

Note: Variables Leaf, Stem, Shoot, Root, Total weights, as well as Leaf count and Leaf area required Log_{10} transformation to meet assumptions of normality. Negative values are a result of the transformations applied to the data.

Table 15. Single factor ANOVA results for *Quercus rubra* seedlings in plots with and without *Microstegium vimineum*. Asterisks (*) signify significant differences.

	M. vimineum presence			
Variable	With	Without	$F_{1,14}$	*p*
Leaf weight (g)	1.489 (0.150)	1.939 (0.237)	2.29	0.153
Stem weight (g)	0.926 (0.078)	1.299 (0.118)	6.19	0.026*
Shoot weight (g)	2.415 (0.210)	3.238 (0.276)	4.99	0.042*
Root weight (g)	4.321 (0.284)	4.790 (0.4.05)	0.94	0.348
Total weight (g)	6.718 (0.461)	7.815 (0.694)	1.60	0.226
Root:Shoot ratio	1.943 (0.095)	1.994 (0.180)	0.06	0.812
Leaf count	6.141 (0.436)	6.639 (0.487)	0.54	0.475
Leaf area (cm^2)	181.310 (22.897)	186.640 (32.815)	0.02	0.903
Mean leaf size (cm^2)	29.071 (2.445)	26.509 (2.993)	0.39	0.544
Stem length (cm)	20.448 (0.806)	22.032 (1.418)	0.93	0.352
Specific leaf weight (mg/cm^2)	0.737 (0.069)	0.790 (0.059)	2.63	0.127

Note: Variable Specific leaf weight required Log_{10} transformation to meet assumption of normality.

during the study, but ocular estimates of insect leaf herbivory appeared similar in plots with and without *M. vimineum*.

Mean *M. vimineum* above-ground biomass, total seed mass, and $\log_{10}$ seed counts did not differ significantly between the different tree species present, or between treatments with and without tree seedlings (Table 16). Mean height of *M. vimineum* did not differ significantly between the mixtures of tree species (Table 17). There was, however, a significant positive linear relationship between the mean tree height and the mean *M. vimineum* height (Fig. 18). Total seed mass per plot was significantly related to total *M. vimineum* biomass per plot (Fig. 19). However, *M. vimineum* $\log_{10}$ seed count per plot was not significantly related to biomass ($R^2 = 0.09$; $F_{1,34} = 3.30$; $p = 0.078$).

Discussion

The lack of any significant differences in PAR suggests that competition for light between tree seedlings and *M. vimineum* was not a major determinant of growth. However, plots with *M. vimineum* had significantly lower percent soil moisture than plots without *M. vimineum*. Therefore, the addition of *M. vimineum* may have reduced soil moisture available to the native hardwood tree seedlings. Reduced soil moisture may partially explain the growth responses in the seedlings. Mean total leaf area per individual is positively related to mean absolute leaf water content (Evans, 1972), and both *A. rubrum* and *L. tulipifera* seedlings exhibited reduced total leaf area (Table 13, 14). Reductions in leaf area suggest that in situations of

Table 16. Single factor ANOVA of *Microstegium vimineum* mean total above-ground biomass (g), seed mass (g), and $\log_{10}$ seed count with native hardwood tree seedlings and in the control (SE).

	Microstegium vimineum		
Tree species	Biomass	Seed mass	Log_{10} seed count
Acer rubrum	213.07 (27.26)	6.26 (0.62)	3.94 (0.08)
Liriodendron tulipifera	155.79 (22.71)	5.23 (1.05)	3.80 (0.10)
Quercus rubra	157.24 (19.90)	5.14 (0.79)	3.86 (0.10)
Control	181.97 (18.66)	6.22 (0.89)	3.94 (0.08)
$F_{3,30}$ (p)	1.53 (0.227)	0.57 (0.642)	0.69 (0.566)

Table 17. Mean (SE) height of *Microstegium vimineum* within mixtures with *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus rubra*.

Species Mixture	Mean Height (Cm)
Acer rubrum	36.40 (2.58)
Liriodendron tulipifera	47.05 (3.24)
Quercus rubra	41.63 (3.23)
Control	45.80 (4.57)
$F_{3,20}$ (p)	1.91 (0.161)

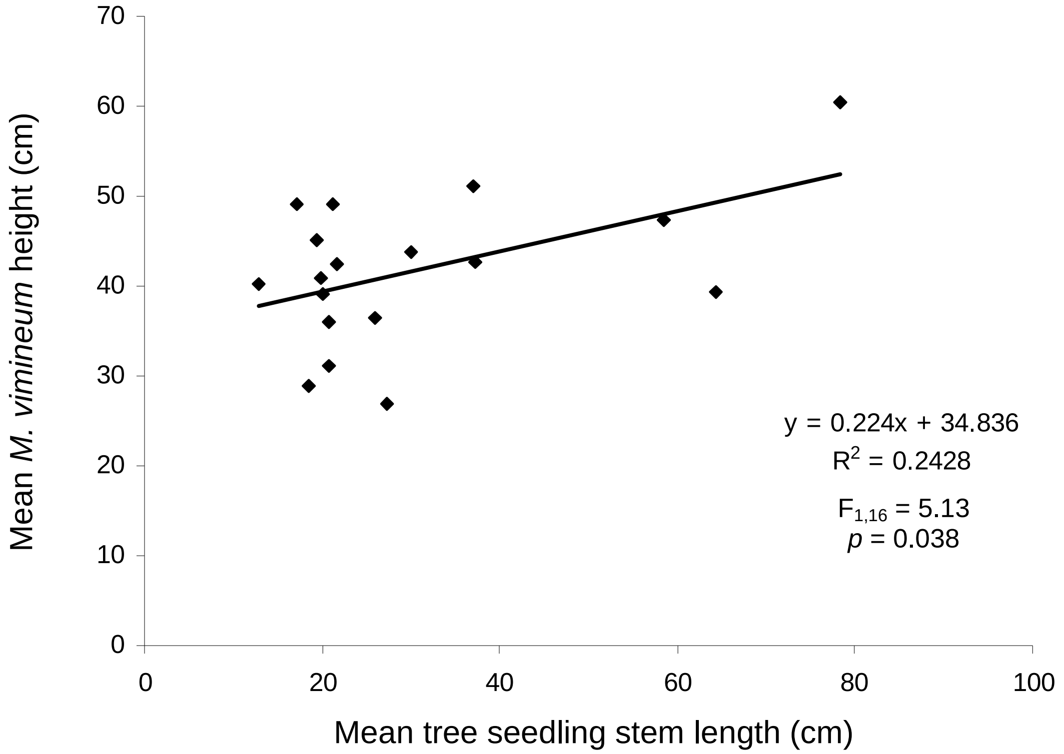


Figure 18. Linear relationship between mean tree seedling stem length and mean height of *Microstegium vimineum* above the soil surface.

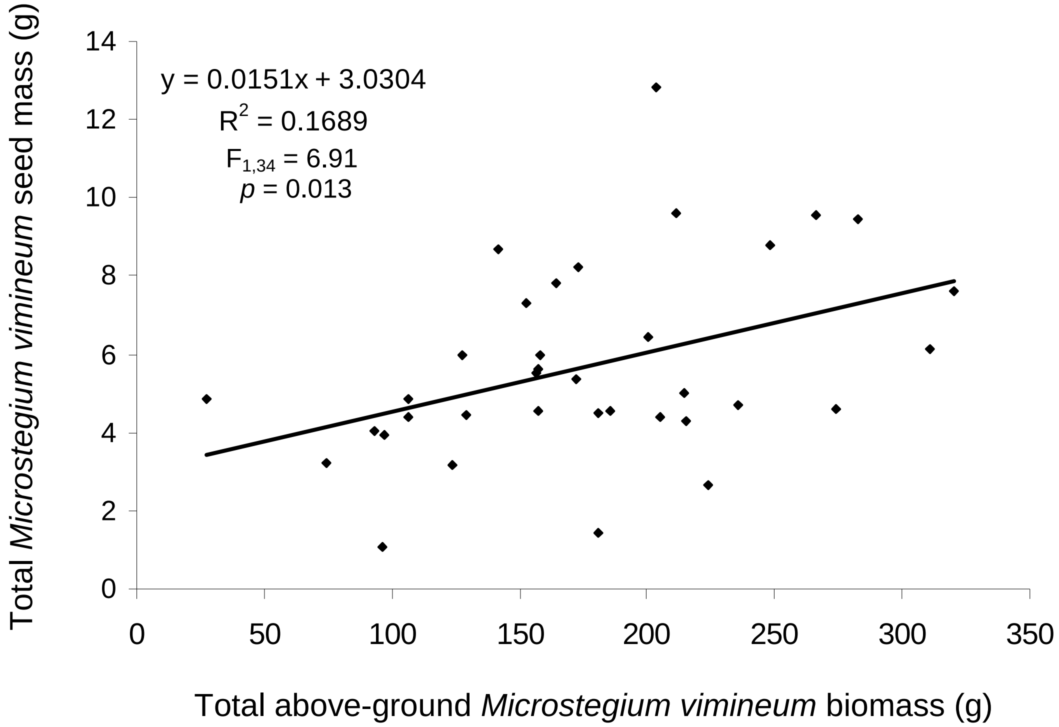


Figure 19. Linear regression model of total biomass and total seed mass per plot for *Microstegium vimineum*.

competition with *M. vimineum*, *A. rubrum* and *L. tulipifera* are at a disadvantage for soil moisture and have reduced leaf area because of the reduced availability of soil moisture. For *L. tulipifera*, this leaf area reduction is similar to previous results presented by Kolb and Steiner (1990). In this study, after a single growing season, *L. tulipifera* leaf area was reduced due to competition with *Poa pratensis* L. (Poaceae) (Kolb and Steiner, 1990).

In addition to soil moisture, *M. vimineum* may have competed with *A. rubrum* and *L. tulipifera* for available soil nutrients. For both of these tree species, there was a reduction in leaf biomass accumulation in plots with *M. vimineum* compared to plots without *M. vimineum* (Table 13, 14). Increases in available soil nutrients can positively affect the mean leaf weight per individual (Evans, 1972). However for *A. rubrum*, this change in leaf weight may be more an effect of leaf area resulting from soil moisture competition and not nutrient reduction because specific leaf weight for *A. rubrum* did not differ between treatments with and without *M. vimineum* (Table 13). The reduction in specific leaf weight for *L. tulipifera* suggests that, unlike *A. rubrum*, there may be impact imposed by *M. vimineum* in terms of competition for soil nutrients (Table 14).

Adequate soil moisture is important during *Quercus* spp. acorn germination and seedling establishment (Pritchard, 1991; Tilki and Alptekin, 2006). However, once the taproot has developed, *Q. rubra* seedlings can survive substantial drought stress (Sander, 1990). Therefore, it is possible that the lack of significant differences in *Q. rubra* leaf area can be attributed to tolerance of drought stress on the part of *Q. rubra*. Alternatively, the limited difference in biomass between *Q. rubra* with and without *M. vimineum* may have been due to the relatively large stores of nutrients within the acorn. While *Q. rubra* stem and shoot weight did differ with and without *M. vimineum*, no other related structures were significantly different between the two treatments (Table 15). Kolb and Steiner (1990) found a different situation with *Q. rubra* and competition with *P. pratensis*, a turf grass. While the levels of biomass accumulation were reduced in shoot weight, leaf area, and stem weight for *Q. rubra* due to grass competition, *P. pratensis* sod was used by Kolb and Steiner (1990). The study presented by Kolb and Steiner (1990) was conducted with much higher turf grass densitis than *M. vimineum* in this experiment, and may explain the differences in *Q. rubra* responses to competition.

It is possible to interpret the responses of the tree species studied in the context of plant strategies. Grime (2001) presented the CSR theory that incorporated competition, stress, and disturbance in an effort to classify species by plant growth strategy as competitors (C), stress-tolerators (S), and ruderals (R). While intermediate strategies exist within this classification, application of the CSR theory to situations of succession can successfully explain observed changes of plant communities along environmental gradients (Caccianiga et al., 2006).

Through the CSR theory presented by Grime (2001), the responses of seedling of these hardwood tree species may be further explained. Compared to other strategies, for example Tilman’s theory on plant strategies (1988), CSR incorporates disturbance and stress into the definition of growth strategies. Tilman (1988) focuses on the long-term consequences of competition within undisturbed sites, however *M. vimineum* establishment and growth are facilitated by disturbance (Chapter II, III). Thus, while disturbance was not included in the manipulative aspects of this study, it is still important to consider disturbance to apply these results to realistic situations. In this situation, the use of Grime’s (2001) CSR theory may be more appropriate.

Acer rubrum resembles the competitor life history strategy. Competitors generally have evolved to utilize resources in environments with low stress and low disturbance, and abundant resources (Grime, 2001). While shade is a stress, competition for light did not appear to be a major determinant in growth in this study. Stress due to moisture competition did appear to be major factor in tree seedling growth. As a competitor, *A. rubrum* is successful in a range of different sites with varying site quality (Walters and Yawney, 1990). Competitor strategies aid such species in acquiring resources in areas that are suitable for most plant species. When fire, a high stress disturbance, is removed from Oak-Hickory forests, *A. rubrum* rapidly increases in numbers to become a dominant species (Albrecht and McCarthy, 2006; Blankenship and Arthur, 2006). In competition with *M. vimineum*, *A. rubrum* may have been at a lesser competitive advantage for soil moisture, at least based on volumetric soil moisture measurements. It was still able to compete for other resources at an intensity that allowed for the similar production of biomass in terms of leaf weight, as compared to *L. tulipifera*, which exhibited decreased leaf weights with *M. vimineum* competition.

Resembling a ruderal species, *L. tulipifera* is more likely to invade sites that have short disturbance rotations. Ruderal species have higher site quality demands than stess-tolerators and usually are less adapted for competition than competitors (Grime, 2001). The rapid utilization of site resources is evident in *L. tulipifera* growth rates. In mean leaf size, *L. tulipifera* leaves grew 3 to 8 times larger than *Q. rubra* and *A. rubrum* (Table 13-15). The stress of reduced soil moisture, and possibly soil nutrients, reduced *L. tulipifera* biomass accumulation in many of the above-ground measures (Table 14). Kolb et al. (1990) also found *L. tulipifera* increased in total dry weight in high moisture and high fertility sites compared to other combinations of high/low moisture and high/low fertility, although these authors considered *L. tulipifera* to be more of a competitor relative to *Q. rubra*. The reductions in moisture in this study as a result of the addition of *M. vimineum* had similar consequences on the biomass accumulation of *L. tulipifera*, resembling the ruderal strategy with limited competitive abilities.

Of the three tree species used in this study, *Q. rubra* most closely resembles the stress-tolerator. *Quercus rubra* has the adapted ability to survive drought conditions once established (Sander, 1990). Leaf variables measured in this study closely related to soil moisture and soil nutrient availability did not differ between areas with and without *M. vimineum* for *Q. rubra* (Table 15). As a drought stress-tolerator, *Q. rubra* would be expected to be able to acquire the necessary resources for growth even with the reduction of soil moisture by *M. vimineum*.

Apparently, none of the species of first-year tree seedlings imposed significant competitive effects on *M. vimineum* (Table 16). While *M. vimineum* above-ground biomass varied between the different tree species and controls, it was not significantly different and seed production did not vary between any species mixtures. Native tree species of this size may not impose enough competitive influence to hinder the spread of *M. vimineum*. Clearly, the situation may be very different with larger saplings and mature trees.

For the purposes of this study, 10 *M. vimineum* individuals were considered equivalent to one tree seedling for planting and maintaining densities. This equivalency was based on leaf area. In this study, PAR was not considered a limiting environmental variable because at all mixtures of *M. vimineum* and tree seedlings there was no significant difference in PAR (Table 11). In terms of root surfaces, however, this equivalency may not hold true, resulting in the differential competitive interactions between *M. vimineum* and native tree seedlings. The differences in density between *M. vimineum* and the tree seedlings may account for why the grass species was able to influence the growth of the tree seedlings, but not vice versa.

The positive relationship between tree stem length and the height of *M. vimineum* above the soil surface (Fig. 18) is most likely related to the growth habit of *M. vimineum*. The individual grass stem lengths ranging from 60-100 cm (Chapter II) result in *M. vimineum* becoming more prostrate, lying on the forest floor. In the study plots, the neighboring tree seedlings provided a support structure that allowed *M. vimineum* to extend a canopy higher above the soil surface (Fig. 18).

A strong linear relationship between *M. vimineum* above-ground biomass and the number of seeds produced has been previously described (Williams, 1998). While a significant regression relationship was not indicated, a similar trend was found in this study. The lack of significance may have resulted from the methodology used. Williams (1998) measured biomass and seed production on an individual plant level, instead of on a plant stand level.

Appling the CSR theory to *M. vimineum* is difficult, and may explain its effectiveness as an invasive species. *Microstegium vimineum* is found in a wide range of habitats from closed canopy forests (Chapter III) to open flood plains (Barden, 1987; Oswalt et al., 2004). In its native range, *M. vimineum* is found in areas with abundant moisture and nutrient availability, in lower mountain regions of Southeastern Asia (Sur, 1985; Osada, 1989). These native habitats suggests that in the habitats it has already invaded, *M. vimineum* has adapted to compete in areas with abundant resources, displaying more of a competitor strategy. However, the annual life history of *M. vimineum* with rapid growth and copious seed production are characteristics of the ruderal strategy (Winter et al., 1982; Williams, 1998; Grime, 2001). Combining competitor characteristics with ruderal characteristics definitely benefits an invasive species introduced into a new range.

The competitive influence imposed by *M. vimineum* varies depending on the species it is interacting with, as illustrated by Leicht et al. (2005) and the results from this study. The short-term nature of the study presented here, and that of Leicht et al. (2005), limits extensive application of the results. Unfortunately, the annual and multimodal growth habit of *M. vimineum* is a hinderance to maintaining precise numbers of this species per plot in multi-year studies. While mortality of tree seedlings was not related to *M. vimineum* competition (Table 8), the altering of biomass accumulation in *A. rubrum* and *L. tulipifera* could have implications for future composition of Central Hardwood forests, particularly if competition with *M. vimineum* persists. Both species are important as dominant and co-dominant canopy trees, which are the defining species for several different forest types (Beckage and Clark, 2003; Schmidt and McWilliams, 2003). The alteration of growth and biomass accumulation in seedlings may in turn alter future forest composition and succession, which exemplifies the need for multi-year studies quantifying the competitive interactions between recurring stands of *M. vimineum* and these native hardwood tree species.

CHAPTER V

INFLUENCE OF *MICROSTEGIUM VIMINEUM* ON INSECT COMMUNITIES IN CENTRAL HARDWOOD FORESTS

Abstract

Plant community structure and richness can greatly influence the distribution and abundance of insects. The addition of exotic plant species to native plant communities can drastically alter vertical structure as well as community richness. *Microstegium vimineum* is an exotic, annual grass that has invaded hardwood forests throughout the Southeastern United States. Four forests, in four separate counties in east Tennessee, were selected and transects were established in areas with and without *M. vimineum*. Along each transect, ten sampling locations were identified. At each sampling location, the plant community was surveyed. Insects were sampled using a terrestrial vacuum sampler three times 6 June to 7 September 2006 with six-week periods between samples. In areas with *M. vimineum*, significantly more herbivores, carnivores, scavengers, and omnivores were collected than in areas without *M. vimineum*. However, it does not appear that the insect community structure changed significantly. Air temperature and relative humidity did not differ significantly between areas with and without *M. vimineum*. These increases in abundance were a result of 2.5 times greater plant cover due to the addition of *M. vimineum* to the plant communities. Insect family richness and diversity were negatively related to plant species richness. The increases in insect abundance due to the presence of *M. vimineum* may not significantly influence the functionality and structure of Central Hardwood forests due to the overall stability of this system type, and certain insectivores may actually benefit from the added structure *M.*

vimineum provides. On the other hand, it is important to note that focusing on a single taxonomic group, such as the insects studied, does not provide a comprehensive measure of exotic species impacts.

Introduction

Insect communities are closely tied to the surrounding plant communities (Haddad et al., 2001; Cagnolo et al., 2002). Changes in plant richness can induce changes in associated insect community structure and abundance, especially in simplified systems with mixtures of few species (Southwood et al., 1979; Risch et al., 1983; Andow, 1990; Knops et al., 1999; Haddad et al., 2001; Crist et al., 2006). While plant diversity has not been shown to unequivocally influence insect abundance, positive relationships have been found between percent vegetative cover and insect abundance (Siemann et al., 1998; Koricheva et al., 2004; Perner et al., 2005; Debano, 2006). The close ecological connection between insect communities and plant communities has resulted in the use of arthropods as indicators of ecosystem function, condition, and integrity (McGeoch, 1998; Weisser and Siemann, 2004; Maleque et al., 2006).

Many human-induced disturbances can alter local plant communities, which, in turn, can change the distribution of insects (Barnes et al., 1998; Schowalter, 2000). The addition of exotic plant species to landscapes can also change local plant communities (e.g. Meiners et al., 2002; Maskell et al., 2006). In some cases, alterations to the surrounding landscape as a result of an exotic plant species introduction and dominance can substantially alter the composition of native plant communities (Mack et al., 2000; Siemann and Rogers, 2006). However, changes to plant communities are often more subtle, and do not necessarily result in restructuring native communities (Mandryk and Wein, 2006). The addition of an exotic plant to the overall community is often associated with some other anthropogenic factor, which, in turn, may be the overarching cause of declines in plant or insect communities (Palmer et al., 2004; Maskell et al., 2006).

One exotic species of growing concern within eastern hardwood forests is *Microstegium vimineum* (Trin.) A. Camus (Poaceae). This C_4 grass species is native to Southeastern Asia and was first collected in North America near Knoxville, TN, in 1919 (Fairbrothers and Gray, 1972; Sur, 1985; Osada, 1989). It is found throughout the Eastern United States from Florida to Massachusetts and as far west as Texas (Fig. 1) (Fairbrothers and Gray, 1972; Hunt and Zaremba, 1992; Redman, 1995; USDA, 2007). *M. vimineum* has become a common target in the control of exotic species throughout its introduced range on both private and public lands (Johnson, 1997*b*; Steele et al., 2006). Although anecdotal information on this species has been sufficient to generate concern, data gained through formal research on the ecological impact of this species in native ecosystems are limited.

Until recently, much of the research associated with *M. vimineum* has focused on the physiology of the plant. *M. vimineum* individuals produce similar amounts of biomass at varying levels of full sunlight (18-100 percent) (Winter et al., 1982). This pattern of biomass production differs from many other C_4 species, which are most often adapted to high-light and high-temperature environments, where reductions in light are accompanied by reductions in biomass production (Winter et al., 1982; Raven et al., 2005). Also, individuals grown under high light levels retain shade-tolerant attributes (Horton and Neufeld, 1998). This light-induced developmental plasticity is evident in the observed ability of *M. vimineum* to readily invade areas altered by natural and human-induced disturbances (Barden, 1987; Cheplick, 2006).

Few studies have been implemented to identify the ecological impacts of *M. vimineum*, however, Cole (2006) found that hardwood tree seedlings might not be recruited into larger size classes due to suppression by *M. vimineum*. Also, increases in *M. vimineum* biomass can reduce height growth of out-planted tree seedlings (Oswalt et al., 2004). In competition with a native grass, *M. vimineum* was superior in resource acquisition, leading to reduced biomass accumulation in the native species (Leicht et al., 2005). In terms of interactions with other exotics, *M. vimineum* appears to have the ability to out compete *Lonicera japonica* Thunb. (Caprifoliaceae) in certain situations (Belote and Weltzin, 2006). Finally, *M. vimineum* did not have an impact on survival of nymphs and larvae of *Ixodes scapularis* Say (Acari: Ixodidae) (Carroll, 2003).

The objectives of this study were to 1) test the hypothesis that insect communities, specifically hexapods, differ in areas with and areas without *M. vimineum* and 2) quantify the ecological impacts of this exotic grass on insect communities within Central Hardwood forests.

Methods

Insect collection forest sites were located in Anderson, Blount, Knox, and Morgan Counties, Tennessee, USA. Patches dominated by *M. vimineum* of sufficient size for multiple samples were selected at each study site and had defined edges were *M. vimineum* did not exist. *Microstegium vimineum* dominance was estimated within each patch to be at least 75 percent through an ocular measurement. Patches were located at the Oak Ridge Forest (Anderson County, TN, 36°0'4" N, 84°13'34" W) and the Cumberland Forest (Morgan County, TN, 36°3'43" N, 84°26'53" W) both managed by the University of Tennessee Forest Resources Research and Education Center, the Ijam's Nature Center Quarry Restoration (Knox County, TN, 35°57'2" N, 85°52'54" W), and Springbrook Park (Blount County, TN, 35°48'4" N83°58'52" W) (Fig. 20). The Anderson County site is actively managed using silvicultural techniques, with recent harvesting activities occurring in 2005 (Richard Evans, personal communication, Univ. of Tennessee). A municipality manages the Blount County site with minimal activity within the forested sampling locations and there appeared to be little recent disturbance (personal observation). A restoration program was initiated in 2001 at the Knox County site by the Ijams Nature Center, which included trail construction and maintenance (James, 2003). Grading of a road at the Morgan County site occurred in 1998, but has remained undisturbed since that time (Martin Schubert, personal communication, Univ. of Tennessee, 5 February 2007).

Study sites were within the Appalachian section of the Central

Figure 20. Insect and plant sampling locations in Anderson, Blount, Knox, and Morgan Counties, Tennessee.

Hardwood forest characterized as being an Oak-Hickory forest type (Fralish 2003). For all four sites, mean annual temperature was 15 ℃, with approximate annual mean total precipitation of 1500 mm at Anderson County, 1300 mm at Blount and Knox Counties, and 1400 mm at Morgan County (NCDC 2005).

A terrestrial vacuum sampler, as described by Harper and Guynn (1998), was utilized to collect insects. Vacuum samples were collected within a bottomless frame box (50 cm X 50 cm X 50 cm). Ten sampling locations were selected on a transect established along the long axis of each patch of *M. vimineum*. At the Anderson and Morgan County sites, large patches of *M. vimineum* existed that accommodated all ten sampling locations within a single patch. Patches of *M. vimineum* at the Blount and Knox County sites were smaller, but were large enough for 3-5 samples per patch. Patches in close proximity at these sites were sampled to approximate the area covered by the large patches in Anderson and Morgan Counties. Control, native forest understory areas without *M. vimineum* were selected along transects within the same forest stand. Ten sampling locations were selected along the control transects at each site.

Three collections were made 6 June to 7 September 2006 with six-week periods between collections. These periods were long enough to ensure recolonization of plots by insects and thus a reasonable level of independence existed between samples obtained on different dates (Tscharntke et al., 2005). Insects were identified to family using Daly et al.

(1998) and Triplehorn and Johnson (2005). Taxonomic arrangement was based on the Integrated Taxonomic Information System (Retrieved: 20 Dec 2006, http://www.itis.gov). Family richness and Shannon-Weaver Diversity Index were calculated for each collection period for each site. Richness (S) was the count of families that were encountered. Shannon-Weaver Diversity Indices were calculated as $H = -\Sigma\, p_i \ln(p_i)$, where p_i = the proportion of the ith family (Hayek and Buzas, 1997). The dominant family feeding guilds were identified using Daly et al. (1998) and Triplehorn and Johnson (2005). The broad feeding guilds were Herbivores (feeding on any part of autotrophic organisms), Carnivores (feeding on any heterotrophic organism through predation or parasitism), Scavengers (feeding on dead organic material), and Omnivores (feeding on a wide range of living and dead organic material).

An herbaceous plant survey was conducted at each sampling location in areas with and without *M. vimineum* in June 2006. Plants were identified to species, except for *Carex*, *Solidago*, *Vaccineum*, and *Viola* species. Percent cover for each species was measured using a point intercept technique within a 0.34 m^2 frame containing 49 points spaced 7 cm apart. Percent plant cover was calculated as the proportion of points intercepted X 100 (Floyd and Anderson, 1987). Percent canopy cover was measured 1 m above the center of each sampling location with a CI-110 Digital Canopy Imager (CID Inc., Camas, WA) in June 2006. Air temperature and relative humidity were measured at the time of insect sampling at five sampling locations in each of the two treatment areas, with and without *M. vimineum*, using a Kestrel 3000 Pocket Weather Meter (Nielsen-Kellerman, Boothwyn, PA).

A nested analysis of variance (ANOVA) was used to identify differences between treatments and sites for percent canopy cover, air temperature, and relative humidity. Log_{10} transformations were used when assumptions of normality were not met. A log likelihood ratio G-test (Sokal and Rohlf, 1995) was used to test the likelihood that abundances of each feeding guild at the sampling locations were independent of treatments with and without *M. vimineum*. A nested ANOVA was used to identify differences between treatments with and without *M. vimineum* for insect richness and diversity with collections at each site analyzed as an independent sample. Simple linear regression was used to test for relationships between insect family richness and diversity and plant species richness and diversity. All analyses were performed with $\alpha = 0.05$.

Results

Percent canopy cover differed significantly between sites with *M. vimineum* and those without *M. vimineum* (Table 18). This difference occurred above and beyond the differences among sites within treatments ($F_{6,72} = 2.84$, $p = 0.016$). Air temperature required Log_{10} transformation due to a non-normal distribution. While differences occurred among sites within treatments for either air temperature and relative humidity ($F_{6,112} = 7.85$, $p < 0.001$; $F_{6,112} = 22.68$, $p < 0.001$, respectively), no significant differences were observed between treatments for both air temperature or relative humidity (Table 18).

Table 18. Mean (SE) percent canopy cover, $\log_{10}$ air temperature, and relative humidity in treatments with and without *M. vimineum*. Asterisk (*) signifies statistically different values.

Variable	With	Without	F_{df}	*p*
Percent canopy cover	75.812 (0.877)	79.428 (0.721)	$11.58_{1,72}$	0.001*
Log_{10} air temperature (°C)	1.432 (0.007)	1.434 (0.006)	$0.03_{1,112}$	0.866
Relative humidity (%)	49.017 (1.206)	49.817 (1.312)	$0.42_{1,112}$	0.518

Plant species richness did not differ significantly between treatments with and without *M. vimineum* (11.75 and 15.50, respectively; $F_{1,6} = 0.94$, $p = 0.370$). Plant species diversity did not differ significantly between treatments with and without *M. vimineum* (1.75 and 1.99, respectively; $F_{1,6} = 0.84$, $p = 0.393$). Percent plant cover was significantly different between treatments; sample locations with *M. vimineum* had a higher percent plant cover than locations without *M. vimineum* (93.52 percent and 36.43 percent, respectively; $F_{1,6} = 64.87$, $p < 0.001$).

A total of 2,839 insects were captured over the three sampling dates in two classes, 11 Orders, and 60 Families (Table 19). Hymenoptera and Collembola were the dominant orders for both areas with and without *M. vimineum* (Fig. 21). Insect family richness did not significantly differ between treatments with and without *M. vimineum* (15.917 and 15.083, respectively; $F_{1,22} = 0.27$, $p = 0.608$). Similarly, insect family diversity did not differ between treatments with and without *M. vimineum* (1.801 and 1.743, respectively; $F_{1,22} = 0.12$, $p = 0.736$).

Feeding guild abundances were not independent of the presence of *M. vimineum* (Table 20). Plant species richness and diversity had negative influences on insect family richness and diversity (Fig. 21). Insect family richness and diversity significantly decreased as plant species richness increased (Fig. 21 A,C). Insect family diversity significantly decreased as plant species diversity decreased, while the relationship between insect family richness and plant species diversity was not significant (Fig. 21 B,D).

Table 19. Numbers of insects in Order and Family across sites and treatments within Anderson, Blount, Knox, and Morgan Counties, Tennessee. Treatments are areas with and without *M. vimineum*. Sampling dates pooled at each site.

Order	Family	Treatment	Anderson	Blount	Knox	Morgan
Archaeognatha	Machilidae	With		1		
		Without	8	4	1	2
Coleoptera	Anthicidae	With				
		Without				1
	Carabidae	With	1	1	8	1
		Without	2	3	2	
	Chrysomelidae	With	4	2	3	1
		Without	3	20	15	1
	Coccinellidae	With		2		
		Without		3	1	
	Cucujidae	With				
		Without		1		
	Curculionidae	With		9	2	5
		Without	13	33	4	
	Elateridae	With			1	
		Without				
	Erotylidae	With				
		Without				1
	Lampyridae	With				1
		Without	1	1	1	
	Nitidulidae	With			1	
		Without	2	3	2	
	Ptiliidae	With	1		1	
		Without		2		
	Staphylinidae	With	1	4	1	8
		Without			3	1
	Tenebrionidae	With				1
		Without				1
Collembola	Entomobryidae	With	107	34	387	65
		Without	118	31	114	23

Table 19 Continued.

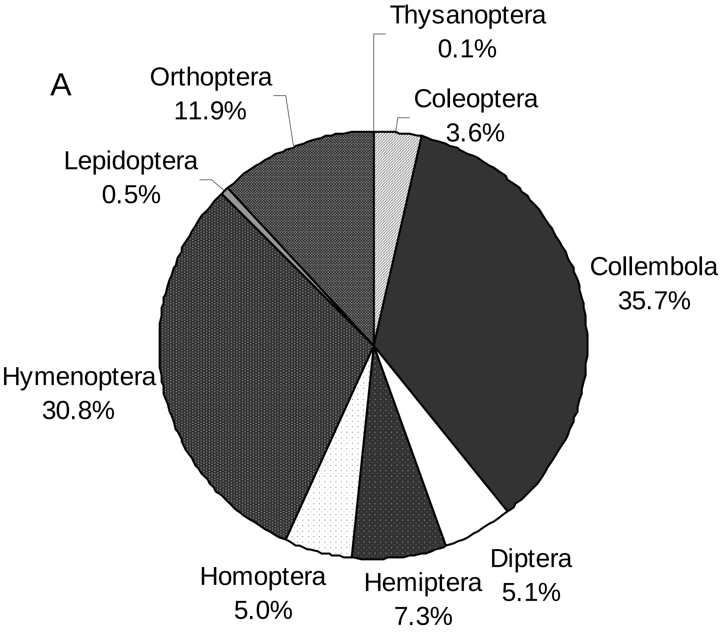
Order	Family	Treatment	Anderson	Blount	Knox	Morgan
Dictyoptera	Blattidae	With	5	2	2	
		Without	21	7	10	8
Diptera	Chamaemyiidae	With				1
		Without				
	Chloropidae	With		17		
		Without	1			
	Culicidae	With			1	
		Without			1	
	Heleomyzidae	With				
		Without				1
	Lauxaniidae	With				
		Without		1		
	Muscidae	With		4		3
		Without		1	1	
	Mycetophilidae	With	6	2	3	6
		Without	2	6		1
	Phoridae	With	2	1		
		Without				
	Piopilidae	With		2		1
		Without		2		1
	Sciaridae	With			1	4
		Without		1	2	
	Sphaeroceridae	With		24	1	
		Without		2	1	
	Stratiomyidae	With			1	
		Without				
	Syrphidae	With			1	
		Without				
	Tephritidae	With		2		1
		Without				
Hemiptera	Cercopidae	With	1			
		Without				

Table 19 Continued.

Order	Family	Treatment	Anderson	Blount	Knox	Morgan
Hemiptera	Cicadellidae	With	23	11	36	7
		Without	5	2	7	
	Coreidae	With	1			
		Without	1	1		
	Flatidae	With				1
		Without	1			
	Lygaeidae	With	25	12	12	22
		Without	6	7	23	2
	Miridae	With	3	11	2	
		Without	1	7	5	
	Nabidae	With	3	4	16	5
		Without	1	1	4	1
	Pentatomidae	With			1	1
		Without	1	1	2	
	Psyllidae	With	1		2	1
		Without	3	3		
	Reduviidae	With	1	1		2
		Without				1
	Tingidae	With		1		
		Without	1			
Hymenoptera	Braconidae	With	1	4		6
		Without		2	3	
	Chalcididae	With				
		Without			1	
	Diapriidae	With				1
		Without		1		
	Eulophidae	With				
		Without	1			
	Eurytomidae	With				
		Without			1	
	Formicidae	With	52	113	73	238
		Without	278	93	92	66

Table 19 Continued.

Order	Family	Treatment	Anderson	Blount	Knox	Morgan
Hymenoptera	Ichneumonidae	With	5	3	3	2
		Without	2	3		2
	Platygasteridae	With		1		
		Without	1			
	Pteromalidae	With		1		4
		Without	2		1	
	Scelionidae	With		1	2	
		Without				
	Sphecidae	WOMV				
		WMV	1			
Lepidoptera	Heliondinidae	With		1		
		Without				
	Lymantriidae	With				1
		Without				1
	Oecophoridae	With	1		2	2
		Without	2			1
Orthoptera	Acrididae	With	11	33	31	10
		Without	3	3	8	3
	Gryllidae	With	4	23	48	26
		Without	6	3	11	3
	Tettigoniidae	With		1		2
		Without				
Plecoptera	Perlidae	With				
		Without	1	1		
Thysanoptera	Thripidae	With		1		
		Without				



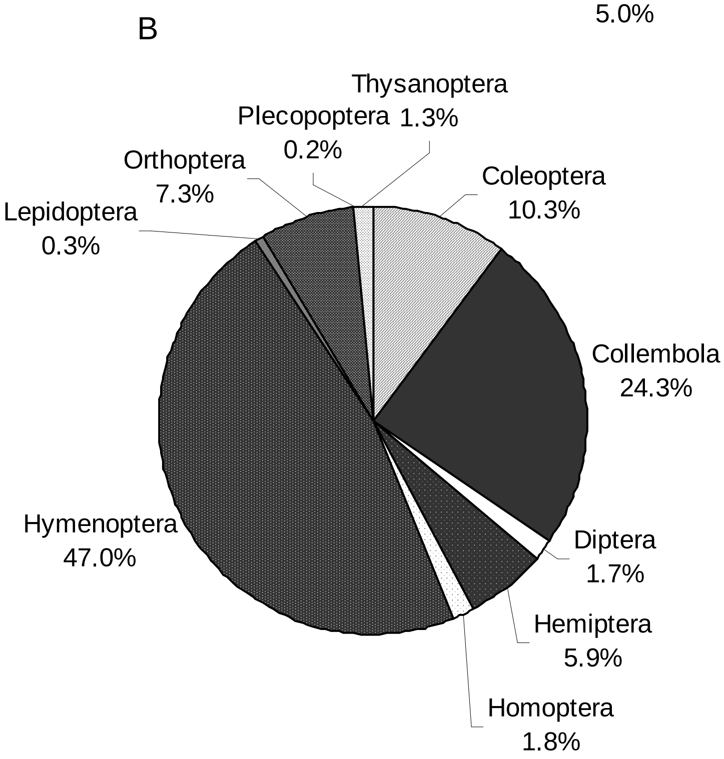


Figure 21. Percentage of all insects collected by order in areas with (A) and without (B) *Microstegium vimineum* in Central Hardwood forests.

Table 20. Log likelihood ratio G-test of insect feeding guild abundances in treatments with and without *Microstegium vimineum*. Asterisk (*) identifies significant G values.

	Abundance			
Feeding Guild	With	Without	$G_{3\ df}$	*p*
			43.02	<0.001*
Herbivores	326	198		
Carnivores	97	56		
Scavengers	661	371		
Omnivores	577	553		
Total	1661	1178		

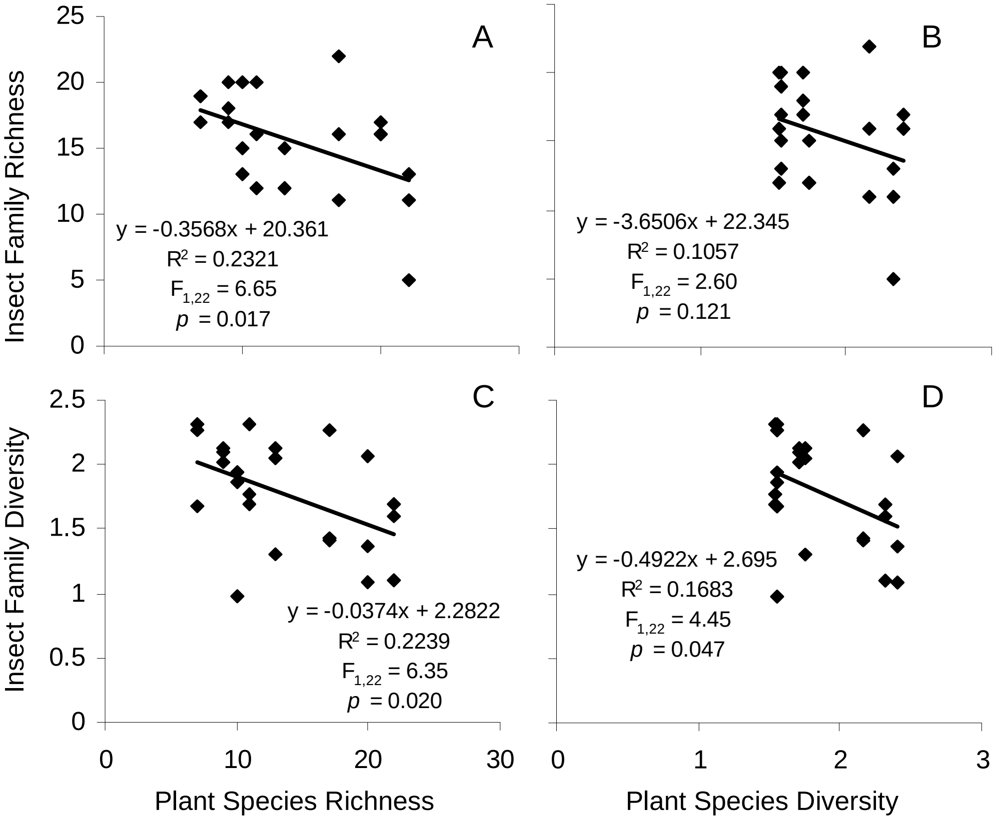


Figure 22. Linear regression of insect family richness and plant species richness (A), insect family richness and plant species diversity (B), insect family diversity and plant species richness (C) and insect family diversity and plant species diversity (D).

Discussion

Quantifying the impacts of exotic plant species on ground and stem dwelling insects can provide further understanding of the total ecosystem alterations imposed by focal exotic species. Within this study, the most visibly obvious difference, as well as statistically significant difference, was the increase in percent plant cover at sites with *M. vimineum* compared to sites without *M. vimineum*. Over 2.5 times more plant cover occurred in areas with *M. vimineum* than in those without, and this increase in plant cover can be attributed to the addition of *M. vimineum* in the plant communities at these sites.

Overall plant species richness and diversity, as well as air temperature and relative humidity, did not differ significantly between treatments with and without *M. vimineum*. Since these environmental factors did not differ between treatments, and insect abundance was not independent of *M. vimineum* presence (Table 16), it may be possible to attribute the general trend of increased insect abundances to the presence of *M. vimineum*. While the insect community total abundance increased, the lack of differences in insect family richness and diversity between treatments with and without *M. vimineum*, as well as the ubiquitous increase in the abundance of each feeding guild and similar dominance of the orders (Fig. 21, Table 20), suggests that the structure of the insect community did not change.

Insects are often suggested for rapid assessment of ecosystem integrity (Tscharntke et al. 1998, Maleque et al. 2006). As an assessment tool, insects allow for rapid collection, rapid processing, especially when identified to family levels, and provide insight into ecosystem function and condition due to their sensitivity to habitat changes (McGeoch, 1998; New, 1998; Gaston, 2000; Cagnolo et al., 2002; Weisser and Siemann, 2004). Insect abundance and diversity are connected ecologically to the level of heterogeneity that occurs in a specific habitat (Southwood, 1977; Lawton, 1983). Maleque et al. (2006) proposed that insect monitoring could effectively evaluate the success of varying ecosystem management techniques, which suggests that success of such management techniques are measured in terms of ecosystem integrity.

Does the increase in insect abundance signal an increase in ecosystem integrity? Or does the change, in either direction, signal a decrease in ecosystem integrity? Answers to these questions are ecosystem dependent. Ecosystems that are sensitive to changes, such as sand dune systems, may be classified as having decreased ecosystem integrity with any change in insect abundances due to the fact that minor changes within the system can significantly alter succession (Johnson, 1997*a*; Lichter, 1998; García-Mora et al., 2000). However, in highly diverse systems, such as Central Hardwood forests, increases in insect abundance, similar to those measured in this study, may not signal decreases in ecosystem integrity due to the fact that minor changes within the system do not significantly alter succession. In fact, in such systems, major changes are necessary, such as the addition or removal of a disturbance, to alter succession (Spetich and Parker, 1998; Pierce et al., 2006).

The influence of *M. vimineum*, in this study, increased the abundance of captured insects. In Central Hardwood forests, it is likely there is a positive relationship between insect abundance and ecosystem function, condition, and integrity, due to the stability and high diversity levels inherent in these forests. If this is the case, then *M. vimineum*, as an exotic plant species, may not cause ecological harm in terms of insect abundance. If there is little or no ecological harm, as indicated by the increases in abundance of insects in this study, then targeting *M. vimineum* for control might not be appropriate and limited resources could be applied to other, more detrimental exotic species. However, utilizing one taxonomic group to measure ecological harm of exotic species might not be the most effective technique. Further research is necessary to fully understand whether or not long-term impacts are imposed by *M. vimineum* within Central Hardwood forests on several key taxonomic groups.

CHAPTER VI

CONCLUSIONS

The research presented here was conducted to identify the factors that facilitate the spread and establishment of *M. vimineum*, as well as what impacts this species is imposing on plant and insect communities, within Central Hardwood forests. This research partially fills a void in the current level of understanding of the ecology of *M. vimineum* in hardwood forests. Prior to the implementation of these studies, there was only anecdotal evidence of how *M. vimineum* becomes established following disturbance and what sites are most susceptible to invasion. Personal observations identified the importance of tip-up mounds, resulting from natural singletree gap formation, as opportunities for *M. vimineum* invasion into interior forests. Combining the results of Chapter II and III with these observations, it is clearer now that spread and establishment of *M. vimineum* into new areas is facilitated by forest floor and soil disturbance. Also, the extent of understanding of *M. vimineum* impacts and influences on plant and insect communities was limited. Chapter IV and V help fill this void and illustrate how *M. vimineum* may be altering future forest composition and insect community structure and abundance in Central Hardwood forests.

Establishment of *M. vimineum* within both forests impacted by timber harvesting and forests without harvesting is facilitated by litter and soil disturbances (Chapter II, III). The addition of canopy disturbance in areas of the forest impacted by harvesting greatly increased the growth rate of *M. vimineum* compared to areas within the same forest where the canopy remained intact (Chapter II). While *M. vimineum* stem length and number of nodes increased with decreasing canopy cover (Chapter II), the nearly closed canopies on the undisturbed sites in Chapter III did not appear to limit its spread. Litter seemed to influence *M. vimineum* establishment to the greatest extent in both field studies. In Chapter II, litter in OPTL and U treatments was the deepest, and *M. vimineum* stem length and percent cover was the least. In Chapter III, control treatments, where litter and soil were not disturbed, had a distance for the farthest individual that was significantly less than either of the two treatments with litter removal. The soil disturbance treatment, where litter was left intact, was not significantly different from the control in any of the spread measures. Therefore, litter appears to play a key role in the rate of spread and establishment of *M. vimineum* in Central Hardwood forests.

These two studies provide insight into the possible locations of invasion and establishment of *M. vimineum* in Central Hardwood forests. While road construction and soil disturbance are inevitably associated with active forest management, focused control, especially of *M. vimineum* already present within a given forest, may slow and limit spread of this exotic species into forest interior areas.

Although insect communities exhibited an increase in abundance related to *M. vimineum* (Chapter V), the reduction in tree seedling growth (Chapter IV) might play a larger role in the possible alteration of future forests within the Central Hardwood region. The proportion of established tree seedlings that are eventually recruited into larger size classes is relatively low compared to the number of seeds that actually germinate (Barnes et al., 1998). Through the reduction in biomass accumulation, *M. vimineum* may be slowly shifting successional patterns by reducing the likelihood that a certain species may recruit into upper strata.

Research Needs

While the research presented here expands upon the current knowledge of how *M. vimineum* becomes established and to what extent it impacts native organisms, there is still a need for further research. A need exists for investigations into the long-term influences imposed by this species and its spatial distribution, as well as defining the specific mechanisms for this species' establishment and spread. Litter appears to be an important factor in the rate of *M. vimineum* spread within Central Hardwood forests, but studies presented here were not designed to identify what mechanisms are occurring to limit spread in the presence of litter. Specifically investigating how seed is trapped, if there are germination issues related to the litter environment, or if there are emergence issues related to litter characteristics would provide further understanding into the environmental factors related to *M. vimineum* invasion. Combining the environmental data collected for Chapter II and III with geographical information systems and available interpolation algorithms, models could be developed to further expand the identification of forested areas that are susceptible to the invasion of *M. vimineum*.

Additional research into the dispersal mechanisms would also be beneficial in identifying forested areas that are susceptible to invasion. It is most likely that the primary dispersal vector of *M. vimineum* seed is water. It is most often found in lower elevations, especially along ephemeral streams. The seeds are easily transported to suitable habitat with moist soils. While flowing water is likely a key dispersal agent, the adhesion of damp seeds to animals is probably an important agent as well. During seed harvesting for the studies presented here, numerous *M. vimineum* seeds adhered to the collectors' arms, especially following precipitation. Dispersal of seed by small to large mammals may explain the isolated patches of *M. vimineum* in interior forest areas on microtopographic features. Trapping studies near established populations of *M. vimineum* may provide answers to questions regarding the amount of seed vectored by wildlife. Also, the use of bulldozers and rubber-tired skidders in timber harvesting operations in forests with *M. vimineum* populations may vector seed in transported mud. Seed transport facilitated by timber harvesting machinery may help explain how *M. vimineum* seed is transported into new forest areas.

The increases in insect abundances presented in Chapter V were a snap shot view of the communities present within Central Hardwood forests invaded by *M. vimineum*. Long-term monitoring of these communities across a larger landscape may provide a clearer understanding as to the true alterations displayed as a result of *M. vimineum* invasion. Although multi-season and multi-year insect monitoring adds complexity to analyzing the resulting community changes due to the sensitivity of insects to various other environmental factors, it will still provide a deeper understanding of the ecology of *M. vimineum*. Also, a more focused survey of insects that feed on

M. vimineum may provide biological control options, leading to a viable control method limiting biomass accumulation of *M. vimineum* and greatly reducing its competitive abilities in relation to native herbaceous and woody species.

Expansion of the research presented in Chapter IV, including additional ecologically and economically important tree species over numerous growing seasons, will also provide more knowledge concerning the importance of *M. vimineum* in forest successional changes.

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APPENDIX A

Appendix A: Annotated plant species list for plots sown with *Microstegium vimineum* within a selective harvest at the University of Tennessee Forest Resources Research and Education Center in Oak Ridge alphabetically by family, genus, and species. The binomial of each taxon and its author is followed by the six disturbance categories in which it was encountered. LS = 1-pass compacted log skid, MPC = multiple-pass compacted, MPL = multiple-pass loosened, OPT = 1-pass compacted track without litter, OPTL = 1-pass compacted track with litter, and U = undisturbed. Each disturbance category is followed by the mean plant species percent cover in quadrats encountered (SE) / the number of quadrats in which that species occurred.

ACERACEAE

Acer rubrum L.; LS 7.22 (5.00) / 4, OPT 2.22 / 1, OPTL 10.56 (6.31) / 4, U 5.19 (0.74) / 3

Acer saccharum Marsh.; LS 2.22 / 1, MPC 3.33 (1.11) / 2, OPTL 4.44 / 1, U 3.33 (1.11) / 2

ANACARDIACEAE

Rhus copallinum L.; LS 5.56 (3.33) / 2, OPT 5.93 (3.70) / 3

Toxicodendron radicans (L.) Kuntze; LS 16.89 (8.15) / 5, MPC 8.00 (2.29) / 5, MPL 12.00 (3.49) / 5, OPT 8.89 (2.22) / 2, OPTL 6.67 / 1, U 17.78 / 1

APIACEAE

Daucus carota L.; MPC 4.44 / 1, MPL 4.44 / 1, OPT 2.22 / 1

ASTERACEAE

Ambrosia artemisiifolia L. ; MPC 15.56 / 1, MPL 4.44 / 1

Erechtites hieracifolia (L.) Raf. ex DC.; LS 2.86 (0.63) / 7, MPC 3.33 (1.11) / 2, OPT 4.44 (1.41) / 5, OPTL 5.93 (1.48) / 3, U 28.89 / 1

Leucanthemum vulgare Lam.; MPC 5.56 (1.11) / 2

CAPRIFOLIACEAE

Lonicera japonica Thunb.; LS 19.63 (4.64) / 6, MPC 21.11 (7.56) / 4, MPL 37.04 (17.51) / 3, OPT 12.78 (5.76) / 4, OPTL 28.89 (3.95) / 4, U 13.33 (7.95) / 5

CELASTRACEAE

Euonymus americana L.; OPT 2.22, OPTL 2.22 / 1, U 8.89 (4.44) / 2

CYPERACEAE

Carex sp. L.; LS 6.67 / 1, MPC 4.44 / 1, MPL 4.44 (2.22) / 2, OPT 3.70 (0.74) / 3, U 4.44 / 1

ERICACEAE

Vaccinium sp. L.; LS 2.22 / 1, U 6.67 / 1

FABACEAE

Cercis canadensis L.; OPTL 6.67 / 1

Desmodium canescens (L.) DC. ; LS 4.44 (1.28) / 3, MPC 8.89 / 1, OPT 2.22 / 1, OPTL 35.56 / 1

Lespedeza cuneata (Dum.-Cours.) G. Don; MPC 23.33 (13.71) / 4, MPL 10.37 (4.51) / 3

Lespedeza repens (L.) W. Bart.; MPL 4.44 / 1

Pueraria montana (Lour.) Merr.; MPC 24.44 / 1, MPL 13.33 / 1

FAGACEAE

Fagus grandifolia Ehrh.; LS 4.44 / 1

Quercus alba L.; LS 7.41 (2.96) / 3, MPC 8.89 / 1, OPTL 4.44 / 1, U 5.56 (3.33) / 2

HAMAMELIDACEAE

Liquidambar styraciflua L.; LS 14.44 (10.00) / 2, MPC 2.22 / 1, OPTL 2.22 / 1

LILIACEAE

Uvularia perfoliata L.; MPL 13.33 (8.89) / 2, U 2.22 / 1

MAGNOLIACEAE

Liriodendron tulipifera L.; LS 4.44 (0.73) / 8, MPL 5.56 (3.33) / 2, OPT 4.44 (2.22) / 2, OPTL 5.19 (1.96) / 3

OLEACEAE

Fraxinus pennsylvanica Marsh.; LS 6.67 (4.44) / 2, MPC 6.67 / 1, MPL 2.22 (0.00) / 2, OPTL 2.22 / 1, U 2.22 / 1

OXALIDACEAE

Oxalis stricta L.; LS 2.22 / 1, MPC 5.08 (1.86) / 7, MPL 5.19 (1.48) / 3, OPT 4.44 / 1

PHYTOLACCACEAE

Phytolacca americana L.; MPC 11.11 / 1, MPL 3.33 (1.11) / 2

POACEAE

Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark; MPC 6.11 (3.89) / 4, MPL 5.19 (1.96) / 3, OPT 4.44 / 1

Dichanthelium clandestinum (L.) Gould; MPL 4.44 / 1

Microstegium vimineum (Trin.) A. Camus; LS 64.44 (8.14) / 15, MPC 97.30 (1.48) / 14, MPL 87.47 (7.96) / 11, OPT 87.88 (6.68) / 11, OPTL 57.28 (13.25) / 9, U 13.33 (7.67) / 12

Poa sp. L.; MPL 11.11 / 1, OPTL 48.89 / 1

POLYGONACEAE

Polygonum pensylvanicum L.; MPL 2.22 / 1

ROSACEAE

Prunus serotina Ehrh.; OPT 6.67 / 1, OPTL 2.22 (0.00) / 2, U 2.22 (0.00) / 3

Rubus sp. L.; LS 6.67 / 1, MPC 3.33 (1.11) / 2, MPL 6.67 (4.44) / 2, OPT 5.56 (2.13) / 4

RUBIACEAE

Galium concinnum Torr. & Gray; OPT 2.22 / 1, OPTL, U 2.22 / 1

SMILACACEAE

Smilax rotundifolia L. ; OPT 2.22 / 1, OPTL 2.22 / 1, U 8.89 / 1

ULMACEAE

Ulmus alata Michx.; OPT 2.22 / 1

Ulmus rubra Muhl.; OPT 2.22 / 1

VITACEAE

Parthenocissus quinquefolia (L.) Planch.; LS 6.39 (1.85) / 8, MPC 2.96 (0.74) / 3, OPT 3.70 (1.48) / 3, OPTL 16.67 (3.80) / 4, U 10.00 (3.33) / 2

Vitis rotundifolia Michx.; MPL 4.44 / 1, OPTL 20.00 / 1

APPENDIX B

Appendix B: Annotated plant species list for plots not sown with *Microstegium vimineum* within a selective harvest at the University of Tennessee Forest Resources Research and Education Center in Oak Ridge alphabetically by family, genus, and species. The binomial of each taxon and its author is followed by the six disturbance categories in which it was encountered. LS = 1-pass compacted log skid, MPC = multiple-pass compacted, MPL = multiple-pass loosened, OPT = 1-pass compacted track without litter, OPTL = 1-pass compacted track with litter, and U = undisturbed. Each disturbance category is followed by the mean plant species percent cover in quadrats encountered (SE) / the number of quadrats in which that species occurred.

ACERACEAE

Acer rubrum ; LS 6.11 (0.53) / 4, MPC 889 (4.44) / 2, OPT 2.22 / 1, OPTL 7.11 (2.85) / 5, U 6.67 (3.39) / 3
Acer saccharum ; MPL 2.22 / 1, OPTL 6.67 / 1, U 5.56 (1.11) / 2

ANACARDIACEAE

Rhus copallinum L.; LS 11.11 / 1, MPC 6.67 / 1, OPT 8.89 (6.67) / 2, OPTL 2.22 (0.00) / 2, U 2.22 / 1
Toxicodendron radicans (L.) Kuntze; LS 23.89 (13.47) / 4, MPC 6.67 (2.30) / 6, MPL 10.00 (4.58) / 4, OPT 17.78 (13.33) / 2, OPTL 14.44 (12.22) / 2, U 14.07 (3.70) / 3

ANNONACEAE

Asimina triloba (L.) Dunal; U 4.44 / 1

APIACEAE

Daucus carota L.; MPC 6.67 (4.44) / 2

ASTERACEAE

Ambrosia artemisifolia L.; LS 4.44 / 1, MPC 2.22 / 1, MPL 8.89 (2.22) / 2
Erechtites hieracifolia (L.) Raf. ex DC.; LS 4.89 (1.63) / 5, MPC 2.22 (0.00) / 2, MPL 2.22 / 1, OPT 12.22 (1.11) / 2, OPTL 4.44 (0.00) / 2
Leucanthemum vulgare Lam.; MPC 5.00 (1.40) / 4

CAPRIFOLIACEAE

Lonicera japonica Thunb.; LS 17.78 (4.63) / 3, MPC 18.33 (4.83) / 4, MPL 30.00 (25.56) / 2, OPT 14.81 (4.86) / 3, OPTL 16.89 (2.57) / 5, U 18.89 (9.67) / 4

CELASTRACEAE

Euonymus americana L.; OPTL 7.78 (3.33) / 2, U 8.89 / 1

CYPERACEAE

Carex sp. L.; MPC 7.78 (3.33) / 2, MPL 7.78 (3.45) / 4, OPT 3.33 (1.11) / 2

DRYOPTERIDACEAE

Polystichum acrostichoides (Michx.) Schott; LS 2.22 / 1

ELAEAGNACEAE

Elaeagnus umbellata Thunb.; LS 2.22 / 1, U 3.33 (1.11) / 2

ERICACEAE

Oxydendrum arboreum (L.) DC.; LS 2.22 / 1
Vaccinium sp. L.; OPTL 24.44 / 1, U 8.89 / 1

FABACEAE

Albizia julibrissin Durazz.; MPL 5.56 (1.11) / 2, OPTL 31.11 / 1
Chamaecrista nictitans (L.) Moench; MPL 2.22 / 1
Desmodium canescens (L.) DC.; LS 8.89 / 1, MPC 4.44 / 1, MPL 4.44 / 1, OPTL 22.22 / 1
Lespedeza cuneata (Dum.-Cours.) G. Don; MPC 3.70 (1.48) / 3, MPL 14.07 (3.92) / 3
Pueraria montana (Lour.) Merr.; MPC 13.33 (6.67) / 2, OPTL 8.89 / 1

FAGACEAE

Quercus alba L.; LS 4.44 / 1, OPTL 2.22 / 1
Quercus rubra L.; OPTL 15.56 / 1

HAMAMELIDACEAE

Liquidambar styraciflua L.; MPC 4.44 / 1, MPL 2.22 / 1, OPT 4.44 / 1, U 2.22 (0.00) / 2

JUGLANDACEAE

Carya tomentosa (Lam. ex Poir.) Nutt.; LS 2.22 / 1

LILIACEAE

Maianthemum racemosum (L.) Link; U 2.22 / 1

MAGNOLIACEAE

Liriodendron tulipifera L.; LS 6.35 (1.41) / 7, MPC 2.22 (0.00) / 2, MPL 2.22 / 1, OPT 18.52 (10.37) / 3, OPTL 6.67 (2.57) / 2

MORACEAE

Morus rubra L.; OPTL 2.22 / 1

NYSSACEAE

Nyssa sylvatica Marsh.; OPT 4.44 / 1

OLEACEAE

Fraxinus pennsylvanica Marsh.; LS 2.22 (0.00) / 2, MPC 11.11 (4.44) / 2, MPL 28.89 / 1, OPT 2.22 / 1, OPTL 4.44 / 1

OXALIDACEAE

Oxalis stricta ; MPC 7.22 (2.46) / 4, MPL 11.11 (8.89) / 2

PHYTOLACCACEAE

Phytolacca americana L.; LS 4.44 / 1, MPC 7.78 (5.56) / 2, MPL 3.33 (1.11) / 2, OPT 6.67 / 1

PLANTAGINACEAE

Plantago major L.; MPC 6.67 / 1

POACEAE

Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark; LS 2.22 / 1, MPC 7.78 (2.31) / 4, MPL 8.89 (3.39) / 3, OPT 2.22 / 1

Microstegium vimineum (Trin.) A. Camus; LS 36.44 (17.67) / 5, MPC 70.32 (9.77) / 14, MPL 86.67 (4.96) / 10, OPT 52.00 (13.13) / 10, OPTL 26.22 (9.82) / 5

Poa sp. L.; MPC 4.44 (0.00) / 2

ROSACEAE

Prunus serotina Ehrh.; LS 5.56 (3.33) / 2, U 4.44 (1.28) / 3

Rosa multiflora Thunb. ex Murr.; OPTL 6.67 / 1

Rubus sp. L.; LS 3.33 (1.11) / 2, MPC 5.56 (1.43) / 4, MPL 9.63 (2.67) / 3, OPT 8.89 (0.00) / 2, OPTL 20.00 / 1

RUBIACEAE

Galium concinnum Torr. & Gray; U 8.89 / 1

SMILACEAE

Smilax rotundifolia L.; LS 5.56 (3.33) / 2, OPT 2.22 / 1, U 4.44 / 1

ULMACEAE

Ulmus rubra Muhl.; MPC 4.44 / 1, MPL 2.22 / 1, OPT 2.22 / 1, OPTL 2.22 / 1

VITACEAE

Parthenocissus quinquefolia (L.) Planch.; LS 11.48 (2.39) / 6, MPC 15.56 / 1, OPT 8.15 (1.48) / 3, OPTL 8.33 (4.19) / 4, U 3.89 (1.06) / 4

Vitis rotundifolia Michx.; LS 2.22 (0.00) / 2, MPL 4.44 / 1, OPT 15.56 / 1, OPTL 2.22 / 1

APPENDIX C

Appendix C: Annotated plant species list for areas with and without *Microstegium vimineum* in Tennessee. The binomial of each taxon and its author is followed by the counties and treatments in which it was encountered A = Anderson, B = Blount, K = Knox, and M = Morgan Counties. 1 = with *M. vimineum* and 0 = without *M. vimineum* treatments. Each county is follwed by the mean plant species percent cover (SE) / the number of quadrats in which that species occurred.

ACERACEAE

Acer negundo L.; K1 2.04 / 1, K0 8.16 / 1

Acer rubrum L.; A0 2.04 / 1, M1 2.04 / 1, M0 5.44 (1.80) / 3

Acer saccharum Marsh.; A0 10.20 / 1, B1 16.33 / 1, B0 2.04 (0.00) / 3, M1 2.04 / 1, M0 2.04 / 1

ANACARDIACEAE

Toxicodendron radicans (L.) Kuntze; A0 8.62 (1.92) / 9, K0 11.22 (4.29) / 4, M1 4.08 / 1, M0 2.04 / 1

APIACEAE

Osmorhiza claytonii (Michx.) C.B. Clarke; K0 4.90 (1.22) / 5

ASTERACEAE

Solidago sp. L.; K1 4.08 / 1

BALSAMINACEAE

Impatiens capensis Meerb.; M1 8.98 (1.04) / 5

BETULACEAE

Ostrya virginiana (P. Mill.) K. Koch; A0 8.16 (4.08) / 2

BIGNONIACEAE

Campsis radicans (L.) Seem. ex Bureau; K1 6.12 / 1

CAPRIFOLIACEAE

Lonicera japonica ; A1 9.30 (2.83) / 9, A0 4.59 (0.59) / 4, B1 17.69 (7.85) / 3, K1 8.16 / 1, K0 4.90 (1.89) / 5

Lonicera maackii (Rupr.) Herder; K1 2.04 / 1

Viburnum acerifolium L.; M0 21.09 (9.52) / 3

CELASTRACEAE

Euonymus americana L.; A1 3.57 (0.98) / 2, A0 3.06 (1.02) / 2, B0 2.04 / 1, M0 4.08 (2.04) 2

COMMELINACEAE

Tradescantia subaspera Ker-Gawl.; M1 2.04 / 1

CONVOLVULACEAE

Calystegia sepium (L.) R. Br.; K1 2.04 / 1

CYPERACEAE

Carex sp. L.; M1 2.04 / 1

DRYOPTERIDACEAE

Polystichum acrostichoides (Michx.) Schott; M0 30.61 (20.41) / 2

ELAEAGNACEAE

Elaeagnus umbellata Thunb.; A1 2.04 / 1, A0 24.49 / 1

ERICACEAE

Vaccinium sp. L.; M0 10.20 / 1

FABACEAE

Cercis canadensis L.; A0 2.04 / 1
Desmodium canescens (L.) DC.; A0 2.04 / 1, M1 2.04 (0.00) / 2
Wisteria floribunda (Willd.) DC.; B0 9.52 (5.57) / 3

FAGACEAE

Quercus alba L.; B1 9.18 (5.10) / 2, B0 11.73 (8.67) / 5, M1 2.04 / 1, M0 12.24 (2.04) / 2
Quercus rubra L.; B0 2.04 / 1
Quercus velutina Lam.; M0 4.08 / 1

JUGLANDACEAE

Carya tomentosa (Lam. ex Poir.) Nutt.; M0 6.12 / 1

LAURACEAE

Sassafras albidum (Nutt.) Nees; M0 24.49 / 1

LILIACEAE

Maianthemum racemosum (L.) Link; A1 2.04 / 1, A0 4.08 / 1, M0 5.10 (1.02) / 2

MAGNOLIACEAE

Liriodendron tulipifera L.; M0 2.04 / 1
Magnolia acuminata (L.) L.; M0 20.41 / 1

NYSSACEAE

Nyssa sylvatica Marsh.; A0 14.29 (4.08) / 2, B0 5.10 (1.02) / 2

OLEACEAE

Fraxinus pennsylvanica Marsh.; A1 8.84 (3.40) / 3, A0 5.44 (2.45) / 3
Ligustrum sinense Lour.; A1 3.06 (1.02) / 2, K0 3.06 (1.02) / 2

OPHIOGLOSSACEAE

Ophioglossum vulgatum L.; B1 4.08 / 1

PINACEAE

Pinus strobus L.; M0 2.04 (0.00) / 2

POACEAE

Microstegium vimineum (Trin.) A. Camus; A1 75.92 (4.06) / 10, B1 76.81 (4.51) / 10, K1 92.65 (2.05) / 10, M1 75.51 (3.33) / 10

POLYGONACEAE

Polygonum persicaria L.; 4.08 / 1

RANUNCULACEAE

Ranunculus sp. L.; A1 4.08 / 1, M1 8.57 (2.84) / 5

ROSACEAE

Agrimonia pubescens Wallr.; A0 6.12 / 1
Duchesnea indica (Andr.) Focke; A1 2.04 / 1, K1 6.71 (1.06) / 7, K0 31.49 (9.31) / 7
Geum canadense Jacq.; K1 2.04 / 1, K0 2.04 / 1, M1 6.12 / 1
Prunus serotina Ehrh.; B0 24.49 (22.45) / 2
Rosa multiflora Thunb. ex Murr.; B0 6.12 / 1
Rubus sp. L.; A0 10.20 / 1, B1 6.12 / 1, M1 6.12 (4.08) / 2

RUBIACEAE

Galium concinnum Torr. & Gray; A1 4.08 / 1
Mitchella repens L.; M0 32.24 (5.71) / 5

SMILACACEAE

Smilax rotundifolia L.; A0 6.12 / 1, M0 4.08 / 1

SOLANACEAE

Solanum carolinense L.; K1 2.04 (0.00) / 3, M1 2.04 (0.00) / 2

ULMACEAE

Ulmus americana L.; A1 4.08 / 1

VIOLACEAE

Viola sp. L.; A1 6.12 / 1, M1 2.04 (0.00) / 2, M0 2.04 / 1

VITACEAE

Parthenocissus quinquefolia (L.) Planch.; A1 7.14 (2.57) / 6, A0 7.00 (2.22) / 7, B1 7.48 (4.46) / 3, B0 12.24 (7.11) / 6, K0 23.27 (15.86) / 5, M1 2.04 / 1

Vitis rotundifolia Michx.; A0 2.04 / 1, B1 2.04 / 1, K0 2.04 / 1, M0 24.86 / 1

VITA

Jordan Michael Marshall was born in 1979 in Lancaster, Ohio. Jordan graduated from New Albany High School in June 1997, and briefly attended Ivy Tech State College in Madison, Indiana. In August 1998, Jordan began attending Ball State University in Muncie, Indiana, where he received his Bachelor of Science degree in Natural Resources and Environmental Management with a minor in Biology in May 2002. Immediately following graduation, Jordan began his graduate studies at Michigan Technological University in Houghton, Michigan. Upon graduation with a Master of Science degree in Forestry from the School of Forest Resources and Environmental Science, Jordan started his doctoral studies at the University of Tennessee, Knoxville. He completed his Doctor of Philosophy in Natural Resources from the Department of Forestry, Wildlife, and Fisheries in the summer of 2007 and assumed the position of Post-Doctoral Research Scientist at Michigan Technological University conducting research on emerald ash borer in Michigan, Indiana, and Ohio.