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**THE ROLE OF ENVIRONMENTAL FACTORS IN THE GROWTH AND
SUPPRESSION OF *MICROSTEGIUM VIMINEUM* (JAPANESE STILTGRASS)**

A Dissertation in
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by
Andrea Nafziger Nord

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The dissertation of Andrea Nord was reviewed and approved* by the following:

David A. Mortensen
Chair of Committee
Professor of Weed Ecology

Margot Kaye
Assistant Professor of Forest Ecology

Larry H. McCormick
Professor Emeritus of Forest Resources

Denice Wardrop
Senior Research Associate
Associate Professor of Geography

David M. Eissenstat
Professor of Woody Plant Physiology
Chair, Intercollege Graduate Degree Program in Ecology

*Signatures are on file in the Graduate School

Abstract

Many invasive plants, including *Microstegium vimineum* (Japanese stiltgrass), are habitat generalists which tolerate a wide range of environmental conditions. This work focused on how environmental conditions affect population growth, abundance, and seed bank persistence of *M. vimineum*, as well as its response to suppression measures.

Patches of *M. vimineum* were planted into five environments and monitored for four years. Population growth tended to be highest in the roadside environment and lowest in intact forest, although due to the variability of the data, these differences were not significant. Small-scale environmental variables, particularly soil moisture and pH, explained much of the variation in final patch size.

To further investigate pH effects, field surveys compared *M. vimineum* along limestone and shale gravel roads. Soil pH along limestone roads was significantly higher than along shale roads as far as 25 m from the road edge. *M. vimineum* occupied significantly more of the roadside area along limestone than along shale roads.

To evaluate the influence of the environment on management outcomes, herbicide and mechanical treatments were applied to *M. vimineum* populations along forest roads, disturbed forest, and wetlands, and plant communities were monitored for three years. Selective herbicide in upland environments did little damage to non-target plant communities while adequately suppressing *M. vimineum*, but mowing was preferable in the wetland environment where the best permissible herbicide also suppresses the non-target plant community.

A buried seed study in the same three environments was used to parameterize population matrix models. Population parameters varied slightly between environments but did not result in different responses to the simulated herbicide scenarios. Biocontrol via a recently discovered pathogen was not sufficient to suppress population growth; however, it allowed a longer interval between herbicide applications in logged and roadside environment.

In conclusion, *M. vimineum* populations do respond to various environmental factors, at least in some instances responding as a beneficiary of ecological changes rather than a primary driver of change. The outcomes of *M. vimineum* suppression efforts are driven less by context-sensitive population dynamics than by the influence of environmental context on choice and efficacy of suppression tactics.

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Preface

Chapter 1 of this dissertation has been published in the journal *Invasive Plant Science and Management*, Volume 3, Issue 1, pages 17-25. The multiple authorship reflects the collaborative nature of research in the Weed Ecology Lab. David Mortensen designed the experiment and commented extensively on the manuscript; Emily Rauschert contributed substantially to the analysis and also commented extensively on the manuscript. All of us participated in discussions of the results and their implications. As primary author I wrote the manuscript, carried out the statistical analysis, and incorporated comments from the other authors and reviewers into the final form of the document. The organization of the paper, with the results and discussion sections combined, follows the format of *Invasive Plant Science and Management*.

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Prologue

Biological invasion, for all the popular and scientific attention surrounding the phenomenon in recent years, is a concept without a clear-cut definition. Valéry et al. (2008) outlined the disagreements in the literature surrounding two commonly cited criteria: first, that a species become established in a new geographical area (i.e. that it is “alien” or “non-native” in a particular place); and second, that its presence cause “major ecological impact.” While there is disagreement over whether native species can also be invasive, and still less consensus on how to measure or define “ecological impact,” by any standards of definition *Microstegium vimineum* (Japanese stiltgrass) is an invasive species.

Discussions of biological invasions often begin with facts or conjecture about how a species moved from its area of origin to a new geographical location. Sakai et al. (2001), in a summary of the biology of invasions, identify the first two steps of invasion as a species surviving transport and successful establishment in new areas. Only a small percentage of potential invasive species survive transport, and only a small percentage of those are able to successfully establish in a new location (Davis 2009). Human activities are now the major disperser of plant species, whether inadvertently through transport of goods such as crop seed contaminated with weed seeds, or deliberately for ornamental planting, erosion control, pasture establishment, etc. (Mack and Lonsdale 2001).

M. vimineum passed the hurdles of both transport and establishment. It is native to a wide swath of Asia, from Japan to India (Barden 1987). It is likely that its seeds were transported to new locations along with the stems and leaves which were used as packing material in the transport of Chinese porcelain (Barden 1987). It was first collected in North America in 1919 near Knoxville, Tennessee, and within the next 20 years was documented in Virginia, Kentucky, Pennsylvania, North Carolina, and Alabama (Fairbrothers and Gray 1972). It is now found in 24 states of the eastern US, from Massachusetts to Illinois and south to Texas and Florida (USDA-NRCS 2011).

Repeated efforts have been made within the history of invasion biology to identify traits that confer “invasiveness”, characteristics which make successful

establishment or a new arrival more likely. Despite the failure to reach any level of predictive ability with this branch of inquiry, there are some traits which are common to many invasive plants. These include rapid dispersal, phenotypic plasticity, capability to produce large quantities of seeds under good conditions but able to produce some seeds even under adverse conditions, abiotic dispersal, and capacity for vegetative reproduction (Alpert et al. 2000, Myers and Bazely 2003).

M. vimineum meets many of these criteria. It is remarkable for the extent of its phenotypic plasticity. It is capable of growing and reproducing under a wide variety of light (Winters et al. 1982), nutrient (Claridge and Franklin 2002), and moisture (Cole and Weltzin 2004) conditions. It gains height and biomass rapidly in the presence of competitors, reducing their growth (Leicht et al. 2005, Belote and Weltzin 2006). Its seed production can be prolific, up to 1000 seeds per plant (Tu 2000).

Another characteristic common to invasive plants that facilitates establishment is freedom from predators and pathogens in their invasive ranges (Keane and Crawley 2002). Not only is *M. vimineum* unpalatable to the major herbivore of eastern forests, white-tailed deer (*Odocoileus virginianus*), the deer can actually facilitate its invasion by selectively browsing native plants, thereby making more resources available to *M. vimineum* (Baiser et al. 2008, Knight et al. 2009). The only pathogen recorded thus far on *M. vimineum* in North America was not observed until 2009, and that only in one location (Kleczewski and Flory 2010).

The stage of invasion labeled “spread” by Sakai et al. (2001) can occur at a variety of spatial scales, both large-scale range expansion and smaller-scale spread of established populations. Spread of *M. vimineum* has been studied at several spatial scales. It has been observed moving with water (Mehrhoff 2000). An analysis of the expansion of small patches determined that natural dispersal alone, estimated at less than 1 m per year, could not account for the spread rates seen at the landscape scale: moving over tens of kilometers within 10-15 years (Rauschert et al. 2010). Another study determined that spread at intermediate scales (tens of meters) can be facilitated by maintenance activities on unpaved forest roads (Rauschert et al. in review). It is clear that *M. vimineum* is dependent on human activities for longer-distance dispersal.

The final stage of biological invasions described by Sakai et al. (2001) is impact, both ecological and economic. Ecological impacts of plant invasions occur at all ecosystem levels: diversity and composition of plant communities (Woods 1993, Higgins et al. 1999, Martin 1999) soil biota and nutrient cycling (Ehrenfeld 2003); and ecosystem-level processes such as hydrologic regimes or fire regimes (Gordon 1998, Brooks et al. 2004).

The ecological impacts of *M. vimineum* on forest and wetland ecosystems have been measured in many components and trophic levels. Belowground, it causes changes in nitrogen cycling, both in wetlands (DeMeester and Richter 2010) and in upland forests (Ehrenfeld et al. 2001); changes in soil pH and litter dynamics (Ehrenfeld et al. 2001); changes in soil microbial community composition and function (Kourtev et al. 2002); and increased abundance of invasive earthworms (Kourtev et al. 1999). Aboveground, it has been implicated in reduced plant community diversity through competitive displacement (Webster 2008). This can contribute to failure of forest regeneration, both natural (Oswalt et al. 2007, Baiser et al. 2008) and planted (Oswalt et al. 2004), with accompanying economic loss. This suppression of forest regeneration by *M. vimineum*, in concert with high deer pressure, can affect other trophic levels as well; it has been implicated in changes to the physical structure of forest, which is very detrimental to some guilds of birds (Baiser et al. 2008).

So the invasion of *M. vimineum* can impact eastern North American forests. Why do we care? Or, as David Mortensen (pers. comm.) perhaps more elegantly phrased it, “We need to articulate why, in a human touched system, we care about a flora that moves toward monoculture.” It could be argued that it is precisely *because* it is a human-touched system that invasive plants are what they are. Decades of fire suppression, high deer pressure, and fragmentation have all played a role. However, we still depend on these ecosystems to provide water, wood, pollination services, regulation of climate, and recreation (Wallace 2007). The process of “biotic homogenization” to which invasive plants contribute can have consequences for ecosystem function and compromise regional ecological resilience (Olden et al. 2004). Furthermore, relatively intact ecosystems and the biodiversity they harbor are

argued by many (this author included) to have some sort of intrinsic value, beyond providing ecosystem services that are of direct benefit to people (Rolston III 1988, Ghilarov 2000).

However varied the motivation, the desire to protect ecosystems frequently translates into practices meant to suppress invasive plants. These practices encompass manual removal, an extremely labor-intensive technique whose accompanying trampling and soil disturbance may in some cases facilitate regeneration of the invasive plant; mechanical techniques such as mowing, which may also be labor-intensive and are not feasible in some kinds of terrain; and chemical control, which is often accompanied by concerns about non-target effects (Myers and Bazely 2003, Smith et al. 2006). Biological control is often considered an attractive option if appropriate organisms can be identified, although this approach also has associated risks of non-target effects, its implementation involves deliberately releasing more non-native species into a region, and many of the biological control agents released to date have failed to impact the density of their targets (Myers and Bazely 2003).

As I was starting my doctoral program, *M. vimineum* interested me as a research topic for several reasons. I had lived in State College from 1996 through 1998 while working on my master's degree. At that time nobody in the area was talking about Japanese stiltgrass; it just didn't seem to be around. When I returned to the area in 2003 it was present throughout nearby Rothrock State Forest, and it was appearing more frequently in the invasive plant literature as well. It seemed a perfect example of many invasive traits: thriving on disturbance, a novel functional type in a forest with few native annual grasses (which primarily consist a few species restricted to specialized conditions), untouched by native herbivores, capable of survival in shade and sun, dry roadsides and wetlands. The wide range of environmental conditions it could tolerate was especially fascinating. Differences in population dynamics between environments has been observed in other invasive plants: dispersal distances in the thistle *Cynara cardunculus* (Marushia and Holt 2006); seedling emergence and establishment in the shrub *Rosa rugosa* (Kollmann et al. 2007); seed mortality rates in the shrub *Ardisia elliptica* (Koop 2004); and survivorship, seed

weight, and seed germination in the forb *Alliaria petiolata* (Byers and Quinn 1998). But very few studies have addressed whether populations of an invasive plant growing in different environments might vary in their response to suppression efforts. It seemed a good candidate for studies of a very applied nature.

The Mortensen lab began an experiment with *M. vimineum* in 2003, inspired by questions of habitat suitability. The Mortensen group hoped to gain information about *M. vimineum* success and failure across a range of habitats or environments that could be used to parameterize a habitat suitability model for the species, of the kind reported in Rew et al. (2005). Therefore, in 2003 they planted patches of stiltgrass into five different environments on the forested slopes above the fields of the Russell E. Larson Experimental Farm at Rock Springs. The first two years of data were written up by Nora Peskin as her master's thesis (Peskin 2005). By the time I joined the project in 2005 it was obvious that this experiment would not lend itself to habitat suitability mapping: while there were some intriguing trends, the variability in patch success within habitat types was just too great.

The first chapter of my dissertation explores that variability in patch success. I looked for patterns in patch success in light of environmental variables measured at the patch level, rather than broad environmental categories. This approach proved successful; a multiple regression model whose most important variables were soil moisture and soil pH accounted for a great deal of the variation in patch success.

The question addressed in the second chapter grew out of reflecting on the importance of soil pH in the patch growth analysis. The presence of both limestone and shale gravel roads through nearby state forests whose soils are naturally acidic offered a “natural experiment” to explicitly test the influence of soil pH on *M. vimineum*.

Suggestions of differences between environments in population growth in the planted patch experiment raised the question of how environmental context might influence responses to suppression measures, both in stiltgrass populations and in non-target plant community. For this field experiment, described in Chapter 3, I established sites in three environments in Rothrock State Forest. Mindful of the high degree of within-environment variability encountered in the Rock Springs trial, I

hoped to minimize that in this experiment by “allowing the stiltgrass to select the sites.” By limiting site selection to areas in which *M. vimineum* had already established dense populations and avoiding areas where its occurrence was sparse, I hoped to be able to focus more clearly on the question of influence of environment.

Another question that grew out of the work in Chapters 1 and 3 was whether *Microstegium* seed bank dynamics differ between environments. Chapter 4 describes a buried seed study carried out on the sites selected for the suppression experiment, which characterizes rates of seed germination, decomposition, and survivorship over three years.

The last chapter is based on a matrix population model which draws from data on fecundity, seed bank dynamics, and *M. vimineum* suppression in the other chapters, to examine how populations respond to various scenarios of herbicide application, a potential biological control pathogen, and a combination of the two.

In general, my goals in this body of work were to explore the interaction between *Microstegium vimineum* and its environment from a number of angles: population growth, seedbank dynamics, and response to suppression. I focused primarily on the scale of *M. vimineum* populations but also stepped back on occasion to consider the broader plant community. In the Epilogue, I reflect on the extent to which these findings inform our ecological understanding of this invasive species and its management.

Literature Cited

Alpert, P., E. Bone, and C. Holzappel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3:52-66.

Baiser, B., J. L. Lockwood, D. La Puma, and M. F. J. Aronson. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. *Biological Invasions* 10:785-795.

Barden, L. S. 1987. Invasion of *Microstegium vimineum* (Poaceae), an exotic, annual, shade-tolerant, C4 grass, into a North Carolina floodplain. *American Midland Naturalist* 118: 40-45.

Belote, R. T., and J. F. Weltzin. 2006. Interactions between two co-dominant, invasive plants in the understory of a temperate deciduous forest. *Biological Invasions* 8:1629-1641.

- Brooks, M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, J.M. DiTomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677-688.
- Byers, D. L., and J. A. Quinn. 1998. Demographic Variation in *Alliaria petiolata* (Brassicaceae) in Four Contrasting Habitats. *Journal of the Torrey Botanical Society* 125:138-149.
- Claridge, K., and S. B. Franklin. 2002. Compensation and plasticity in an invasive plant species. *Biological Invasions* 4 339-347.
- Cole, P. G., and J. F. Weltzin. 2004. Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeastern Naturalist* 3:545-562.
- Davis, M. A. 2009. *Invasion Biology*. Oxford University Press, Oxford, UK.
- DeMeester, J. E., and D. B. Richter. 2010. Differences in wetland nitrogen cycling between the invasive grass *Microstegium vimineum* and a diverse plant community. *Ecological Applications* 20:609-619.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503-523.
- Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11 (5) 1287-1300.
- Fairbrothers, D. E., and J. R. Gray. 1972. *Microstegium vimineum* (Trin.) A. Camus (Gramineae) in the United States. *Bulletin of the Torrey Botanical Club* 99 97-100.
- Ghilarov, A. M. 2000. Ecosystem functioning and intrinsic value of biodiversity. *Oikos* 90:408-412.
- Gordon, D.R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. *Ecological Applications* 8:975-989.
- Higgins, S.I., D.M. Richardson, R.M. Cowling, and T.H. Trinder-Smith. 1999. Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology* 13: 303-313.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17:164-170.
- Kleczewski, N. M., and S. L. Flory. 2010. Leaf blight disease on the invasive grass *Microstegium vimineum* caused by a *Bipolaris* sp. *Plant Disease* 94:807-811.
- Knight, T. M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal* 29:110-116.
- Kollmann, J., L. Frederiksen, P. Vestergaard, and H. H. Bruun. 2007. Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biological Invasions* 9:31-42.

- Koop, A. L. 2004. Differential seed mortality among habitats limits the distribution of the invasive non-native shrub *Ardisia elliptica*. *Plant Ecology* 172:237-249.
- Kourtev, P. S., J. G. Ehrenfeld, and M. Haggblom. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83:3152-3166.
- Kourtev, P. S., W.Z.Huang, and J.G.Ehrenfeld. 1999. Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. *Biological Invasions* 1:237-245.
- Leicht, S. A., J. A. Silander, and K. Greenwood. 2005. Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus. *Journal of the Torrey Botanical Society* 132:573-580.
- Mack, R. N., and W. M. Lonsdale. 2001. Humans as Global Plant Dispersers: Getting More Than We Bargained For. *BioScience* 51:95-102.
- Martin, P. H. 1999 Norway maple (*Acer platanoides*) invasion of a natural forest stand: understory consequences and regeneration pattern. *Biol. Invasions* 1:215–222.
- Marushia, R. G., and J. S. Holt. 2006. The effects of habitat on dispersal patterns of an invasive thistle, *Cynara cardunculus*. *Biological Invasions* 8:577-593.
- Mehrhoff, L. J. 2000. Perennial *Microstegium vimineum* (Poaceae): An apparent misidentification? *Journal of the Torrey Botanical Society* 127:251-254.
- Myers, J. H., and D. R. Bazely. 2003. *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge, UK.
- Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution* 19:18-24.
- Oswalt, C. M., W. K. Clatterbuck, S. N. Oswalt, A. E. Houston, and S. E. Schlarbaum. 2004. First-year effects of *Microstegium vimineum* and early growing season herbivory on planted high-quality oak (*Quercus* spp.) seedlings in Tennessee. *Proceedings of the 14th Central Hardwoods Forest Conference*, pp 1-9.
- Oswalt, C. M., S. N. Oswalt, and W. K. Clatterbuck. 2007. Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *Forest Ecology and Management* 242:727-732.
- Peskin, N. 2005. Habitat suitability of Japanese Stiltgrass *Microstegium vimineum* in an Appalachian forest. M.S. The Pennsylvania State University.
- Rauschert, E. S. J., D. A. Mortensen, O. N. Bjornstad, A. N. Nord, and N. Peskin. 2010. Slow spread of the aggressive invader, *Microstegium vimineum* (Japanese stiltgrass). *Biological Invasions* 12:563-579.
- Rolston III, H. 1988. *Environmental Ethics: Duties To and Values In the Natural World*. Temple University Press, Philadelphia PA.

- Rew, L.J., B.D. Maxwell and R. Aspinall. 2005. Predicting the occurrence of nonindigenous species using environmental and remotely sensed data. *Weed Science* 53:236-241
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305-332.
- Smith, R. G., B. D. Maxwell, F. D. Menalled, and L. J. Rew. 2006. Lessons from agriculture may improve the management of invasive plants in wildland systems. *Frontiers in Ecology and the Environment* 4:428-434.
- Tu, M. 2000. Element stewardship abstract for *Microstegium vimineum*. The Nature Conservancy.
- USDA-NRCS PLANTS Database. 2011. PLANTS Profile for *Microstegium vimineum* (Trin.) A. Camus. <http://plants.usda.gov/java/profile?symbol=MIVI> Accessed 4-25-11.
- Valéry, L., H. Fritz, J.-C. Lefeuvre, and D. Simberloff. 2008. In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions* 10:1345-1351.
- Wallace, K. J. 2007. Classification of ecosystem services: Problems and solutions. *Biological Conservation* 139:235-246.
- Webster, C.R., J.H. Rock, R.E. Froese, and M.A. Jenkins. 2008. Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10-year results. *Oecologia* 157:497-508.
- Winters, K., M. R. Schmitt, and G. E. Edwards. 1982. *Microstegium vimineum*, a shade adapted C4 [carbon pathway] grass [Comparison of growth with *Digitaria sanguinalis* and *Sporobolus airoides*]. *Plant Science Letters* 24:311-318.
- Woods, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. *Am. Midland Nat.* 130, 62-74.

Chapter 1

Environmental factors influence early population growth of

Microstegium vimineum (Japanese stiltgrass)¹

Andrea N. Nord, David A. Mortensen, and Emily S.J. Rauschert

Abstract

Habitat suitability and disturbance can shape the early stages of biological invasions in important ways. Much that we know about habitat suitability and invasion originates from correlative studies, which provide a point-in-time characterization of invasive plant abundance and associated site characteristics. In our study, we test the influence of habitat suitability by creating small-scale invasions in a range of habitat types. Thirty patches of the invasive annual *Microstegium vimineum* were planted into six habitats in a deciduous forest in central Pennsylvania and patch growth was monitored for four years. Each of the thirty sites included a subplot subjected to litter disturbance at time of planting. This litter disturbance led to increased seedling recruitment only in the first two years. While patches were generally larger in wetland and roadside habitats, site influence was highly variable. Environmental variables (soil moisture, ammonium-N, pH, and plant species richness) measured in each plot proved better predictors of population success than broad habitat categories. We conclude that risk assessment for species such as *M. vimineum* should focus not on habitat types, but on areas likely to experience the physical changes that release *M. vimineum* populations.

Introduction

Understanding the early stages of biological invasions is crucial to understanding the entire invasion process. However, these stages of the invasion process are poorly understood (Crooks and Soule, 1999). They are difficult to study,

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and may be of short duration so are often overlooked (Marchetti et al., 2004). Studies involving deliberate introduction of invasive species into the environment to monitor their early growth (e.g. Meekins and McCarthy, 2001; Tanentzap and Bazely, 2009) are understandably rare. However, improving both preventive management and predictive modeling may require better understanding of the early stages of invasion.

A variety of factors may influence the early population growth of invasive plants. Differences in habitat type, which can encompass many factors such as light and water availability, soil characteristics, and the nature of the surrounding plant community, have been shown to affect population metrics of some species. For example, habitat effects have been demonstrated in germination of the invasive shrub *Ardisia elliptica* in Florida (Koop, 2004) and seedling survival and growth and response in disturbance of *Rosa rugosa* in Denmark (Kollmann et al., 2007). In different habitats, *Alliaria petiolata* shows differences in survival and growth (Meekins and McCarthy, 2001) and fruit production (Byers and Quinn, 1998).

It is also important to recognize that both the importance of environmental factors and the environments themselves can change over the course of the invasion. Therefore, information gained by studying long-established invasive populations may not be applicable to early stages. Jongejans et al. (2007) observed changes in the availability of suitable microsites throughout a 7-year study of experimentally planted populations of *Carduus acanthoides*. Wisser et al. (1998) analyzed data spanning 23 years in a New Zealand forest being invaded by the understory herb *Hieracium lepidulum*. At the end of the study the best predictors of site invasion were plant species richness and soil fertility. However, the early stages of site invasion were highly influenced by dispersal limitations: distance of the sites from potential propagule sources was quite important.

More detailed understanding of the effects of habitat and other environmental factors on the early stages of invasion could improve efforts at risk assessment mapping. This approach uses data about invasive species responses to environmental factors or habitat types, as well as spatial information about the distribution of these factors in the landscape to identify areas most susceptible to invasion by the target

species. These maps can then be used to guide sampling and control efforts (Radosevich et al., 2007).

Microstegium vimineum (Trin.) A. Camus (Japanese stiltgrass, Nepalese browntop) is an annual grass that is highly invasive in many habitats in the eastern US: river banks, roadsides, shallow wetlands, floodplains, and forests (Hunt and Zaremba, 1992; Redman, 1995). In general *M. vimineum* prefers moist but not saturated soils (Tu, 2000), but it can tolerate a broad range of environmental conditions (Cole and Weltzin, 2004) and can reproduce in both shade and sun (Winters et al., 1982). It is reported to reduce native plant diversity (Oswalt et al., 2007), interfere with timber regeneration (Oswalt et al., 2004), and affect soil properties such as nutrient cycling (Ehrenfeld et al., 2001).

Disturbance is an environmental factor that can greatly increase *M. vimineum* spread and establishment (Marshall and Buckley, 2008). Human activities are the most important means of seed dispersal, along with moving water (Mehrhoff, 2000; Rauschert, 2008). Barden (1987) observed slow establishment on undisturbed sites, but vigorous spread on soils scoured by floods. Roads and trails are important points of establishment (Cole and Weltzin, 2004).

In order to obtain information about which habitat types permit greater *M. vimineum* reproductive success and dispersal in early invasion stages, we deliberately initiated “invasions” of *M. vimineum* by planting patches into six different habitats. We disturbed the litter layer in subplots at planting to investigate the role of disturbance in early establishment. We hypothesized that 1) patch growth would differ between habitat types, resulting in larger populations in roadside and disturbed forest habitats and smaller populations in intact forest; and 2) litter disturbance would increase patch growth.

Methods and Materials

Study Site

The study was conducted on a forested portion of The Pennsylvania State University’s Russell E. Larson Agricultural Research Center at Rock Springs,

Pennsylvania, USA (40.71161° N, 77.93067° W). The research center is located in central Pennsylvania's ridge and valley physiographic province at an approximate elevation of 365 m. Yearly precipitation averages 933 mm; temperatures range from an average minimum of -6.7° C in January to an average maximum of 28.1° C in July (Braker, 1981). Extensive searching throughout the study area during the 2002 growing season found no *M. vimineum* present.

Six habitat types were selected. Roadside (R) habitat plots were located along an unpaved, limestone graveled road through second-growth deciduous forest. The road had a 10-15% grade, received little maintenance, and was used primarily by research farm equipment. The soil type is a Murrill very stony silt loam, a well-drained soil from sandstone colluvium and limestone residuum. The intact forest habitat was second-growth dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), and white pine (*Pinus strobus*). These plots were on Laidig extremely stony loam, well-drained soil from sandstone and siltstone colluvium. Intact forest sites with understory (IFU) and with no understory (IFN) were selected. The disturbed forest habitat was similar in species composition to the intact forest, but selective logging occurred on the site 15-20 years prior to the experiment. Plots in the disturbed forest with understory (DFU) and with none (DFN) were established. The wetland habitat (W) was an open wet meadow dominated by sedges (*Carex* spp.) and goldenrods (*Solidago* spp.) The DFN, DFU, and W plots were on Andover channery and very stony loams, poorly-drained soils formed from sandstone, siltstone and shale colluvium (all soils information from Braker, 1981).

Experimental Design and Data Collection

Five plots were established in each of the six habitat types. Plots within each habitat type were located within 10-20 m of each other; the location of habitats in the landscape did not allow blocking. Each 1 x 2 m plot was divided into two 1 m² treatment sub-plots. One sub-plot in each plot was left undisturbed, and the other was subjected to a light disturbance at the time of planting: the litter layer was raked with steel garden rakes. Litter was not removed, and disturbance to the soil was minimal. Each subplot was sown in April 2003 with 300 *M. vimineum* seeds obtained the

preceding fall from naturally occurring populations in a nearby state forest. Vegetation already present in the plots was not removed.

To assess seedling recruitment we counted all emerged *M. vimineum* in each subplot in early June, beginning in 2003. By the second year seedlings were also found outside the original plots, and these were counted as well. Hereafter the entire population of *M. vimineum* at a plot, including both sub-plots as well as those plants that had spread into the surrounding area, will be referred to as a “patch”.

To assess seed production in each patch we destructively sampled in late September; *M. vimineum* plants produce seed heads in each leaf axil and must be dissected for seed counting. In 2003 and 2004 each sub-plot was divided into fourths, and all above-ground plant matter in two diagonally-opposite quarters was harvested for counting. Plant matter for seed counting in 2004 was taken from the quarters not used in 2003 (Peskin, 2005).

Plots established in the disturbed forest with understory (DFU) habitat could not be surveyed after 2004 due to vigorous growth of *Rosa multiflora* (multiflora rose). When the experiment was terminated in 2006, we ascertained with some difficulty that there was no surviving *M. vimineum* in these plots.

Environmental data was collected at each plot in 2004. Soil samples were sent to the PSU Agricultural Analytical Services Laboratory (State College, PA) where they were analyzed for pH, P, K, Mg, Ca, NH₄-N, NO₃-N, and soil organic matter. Other variables measured included canopy cover, soil chemistry, and visual estimates of percent litter and vegetation cover. Canopy cover was estimated photographically by leveling a tripod-mounted camera¹ in the center of each plot and exposing a nadir view image looking up into the forest canopy. Images were processed digitally with Photoshop² to determine percent of view filled by tree canopy. Percent litter cover was visually estimated. Plant community within each plot was characterized by recording percent cover by species.

In 2006 all previous measurements were repeated in the plots. In addition, soil moisture was measured in each sub-plot in July 2006 with an volumetric soil moisture probe³. This was done only once, with the purpose of comparing plots and not to describe moisture regimes over time.

Patches were sprayed with the grass-specific herbicide sethoxydim in 2006 before seed production occurred. The patches continue to be monitored yearly, with spraying and hand-weeding as needed to complete the eradication phase of the experiment.

Statistical Analysis

We used repeated measures ANOVA to address the questions of habitat influence and population change over time. The response variable, total patch seedling recruitment, was log-transformed to improve normality (Quinn and Keough, 2002). Plot was treated as random in a mixed-effects model.

We did not expect the effects of the disturbance treatment to be constant throughout the course of the experiment as it was not intense and occurred only once. Furthermore, we wanted to test for a habitat-disturbance interaction. Therefore we performed separate, factorial ANOVAs for log-transformed seedling counts for each year and log-transformed seed production estimates for 2003 and 2004, with disturbance and habitat as factors. For this analysis we used counts of seedling recruitment only within the original planted subplots, disregarding all seedlings counted outside the original plots.

To examine the predictability of trajectories over time, seedling counts in each year were compared to seedling counts in the following year with simple linear regression.

We used a “best subsets” algorithm (Neter et al., 1996) to explore the importance of environmental variables on population metrics for the two years (2004 and 2006) in which environmental data were collected. Free predictors included all above-mentioned environmental variables, with plant community information represented as percent cover of woody plants and of other graminoids in the plant community, as well as species richness. As complete environmental data was only available for 2004 and 2006, this analysis was conducted with 2004 total stem counts, 2004 seed counts, and 2006 stem counts as response variables. All response variables were log-transformed to improve normality. Adjusted- R^2 and Mallows C-p values were used to select the best model for each response variable. Once predictor

variables were selected with the “best subsets” algorithm, they were used in linear multiple regression models.

To avoid multicollinearity, we checked correlations of all variables prior to beginning the “best subsets” algorithm. Several soil chemistry measurements in the 2004 data were highly correlated; we excluded Ca, Mg, K, and NO₃-N from the pool of potential predictors as they were highly correlated with pH or NH₄-N. Variables were less correlated in the 2006 data so no variables were removed. We also checked variance inflation factors of the final regression models to ensure they were below 10 (Quinn and Keough, 2002)

Mixed-effects repeated measures ANOVAs were performed with JMP⁴; Minitab⁵ was used for best subsets regressions; and R6 was used for all other models. Alpha levels were set at $p < 0.05$ in all statistical tests.

Results and Discussion

Habitat Effects

Visualization of the 2006 seedling counts by habitat type (Figure 1.1) shows a great deal of variability but does suggest trends: final *M. vimineum* counts tended to be very high in roadside (R) patches, moderately high in wetland (W) patches, and low in disturbed forest (DFU) and intact forest with understory (IFU) patches. However, these trends were not statistically significant (Table 1.1).

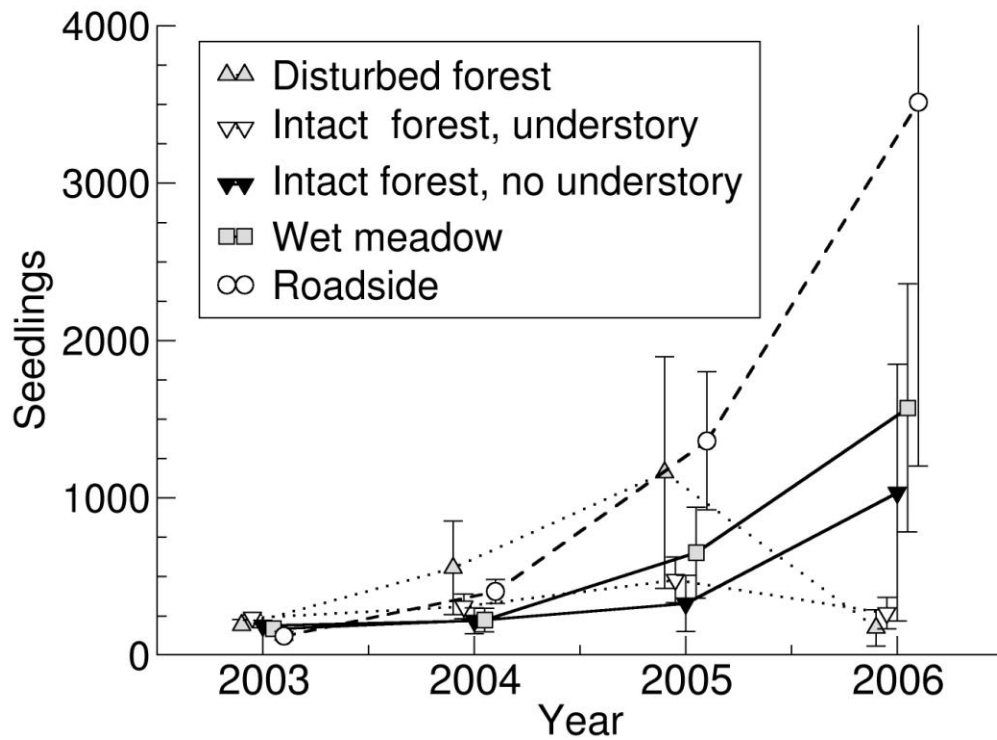


Figure 1.1. Seedling recruitment counts by habitat. Bars represent standard error.

Source	Df	Sum of Squares	Mean Squares	F ratio	P
habitat	4	14.7139	3.67848	1.13169	0.2978
plot[habitat]	20	55.8656	2.79328	4.6153	<0.0001
year[habitat, plot]	25	69.4838	2.77935	4.5922	<0.0001
Error	50	69.4838	0.60523		
Total	99	170.3247			

Table 1.1. Repeated measures ANOVA to test effect of habitat. Plot was treated as a random effect.

The high seedling counts in the roadside patches are consistent with work by Christen and Matlack (2009) showing higher *M. vimineum* germination and growth in patches planted on roadsides than in intact forest. They conclude that roadsides function as ideal habitat for this species, and attribute this to greater canopy openness. However, the road in our study was narrow and surrounded by mature second-growth forest, and canopy openness there was not significantly higher than in any other habitat. In our study the success of the roadside patches is likely due to the increased disturbance associated with road use. The response of *M. vimineum* to disturbance is well documented (Barden, 1987; Marshall and Buckley, 2008; Oswalt and Oswalt, 2007). Elevated pH from the limestone gravel may also have been a factor; this variable is treated in more depth below. The vigorous growth of *M. vimineum* on roadsides is a management concern because it has also been established that this species disperses well along roads (Mortensen et al., 2009), and that propagules can move off the roads into the forest interior (Cole and Weltzin, 2004).

The patches in the disturbed forest without understory were experiencing population declines by the end of the experiment. This was due to the spread of *Rosa multiflora*, the invasive shrub that completely overgrew the patches in the disturbed forest with understory habitat. Other studies have also noted that *M. vimineum* is limited by dense shade from mid-canopy woody plants (Barden, 1987; Cole and Weltzin, 2005).

The high degree of within-habitat variability in patch success highlights the importance of microsite factors to early *M. vimineum* success, and underscores the idea that broad-scale habitats as we perceive them are not necessarily relevant to how *M. vimineum* experiences its environment. At the same time, the pattern of variability we observed is reminiscent of the epidemiological concept of “super-spreaders.” In epidemiology, super-spreaders are individuals which spread infection at a much greater rate than average (Li et al., 2004). Similarly, in this experiment we observed that each habitat type contained one or two patches whose patch scale fecundity and seedling counts were much greater than others in their habitat type, often by an order of magnitude. Even among the top-performing patches from each habitat there were striking inequalities: in 2005, patch R5 produced ten times as many seeds as the next

most productive patch IFN4. Our data raise the intriguing possibility that a few “super-spreading” patches may have a disproportionate influence in the process of species invasion, either due to faster than average spatial spread or higher than average propagule production.

Disturbance Treatment

Litter disturbance at the time of planting resulted in significantly greater seedling recruitment in the first two years of the experiment (Table 1.2). However, there were no differences between disturbed and undisturbed subplots in subsequent years. Seed production was higher in disturbed subplots only in the first year. The disturbance by habitat interaction term was not significant in any year for either seeds or stems; these portions of the models are not shown.

Others have noted increased recruitment of *M. vimineum* following litter disturbance (Marshall and Buckley, 2008; Oswalt and Oswalt, 2007). The magnitude of *M. vimineum* response reported in these papers is much greater than what we observed; but their disturbance events were more intense than ours. We saw a stronger effect on recruitment than on seed production, suggesting that disturbance has a stronger impact on non-reproductive stages of this species’ life cycle.

	Year	Source	DF	Sum of Squares	Mean Squares	F Ratio	P
Recruitment	2003	Treatment	1	3.225	3.225	60.144	<0.001
		Residuals	48	2.574	0.054		
	2004	Treatment	1	1.353	0.353	5.709	0.021
		Residuals	48	11.374	0.237		
	2005	Treatment	1	0.063	0.063	0.136	0.714
		Residuals	48	22.128	0.461		
2006	Treatment	1	0.018	0.018	0.030	0.864	
	Residuals	48	29.166	0.608			
Seed Production	2003	Treatment	1	4.885	4.885	3.917	0.054
		Residuals	48	59.870	1.247		
	2004	Treatment	1	0.809	0.809	0.971	0.330
		Residuals	48	39.987	0.833		

Table 1.2. ANOVA models showing effect of disturbance treatment on seedling recruitment and seed production.

Our finding that the effect of disturbance decreases with time suggests possible management strategies. Disturbances of forest systems may be inevitable, but they may not render the plant communities more invulnerable indefinitely. In events such as logging with equipment contaminated with seed, propagule delivery occurs at the same time as soil disturbance. If methods could be found that decouple propagule delivery from disturbance, such events might not necessarily result in invasion.

Population Trajectories

M. vimineum germinated in all surveyed patches in all years. However, only six patches showed increases in every year: two in IFN, one in W, and three in R. Two patches, one in each intact forest type, showed consistent declines, and the remaining 17 patches showed mixed patterns of increases and decreases from year to year. Seeds were produced in all patches in all years with the exception of one wet meadow patch, which set no seeds the first two years.

Seedling counts were not highly correlated with counts in the same patches the following year (average adj.- R^2 for all consecutive pairs of years = 22.0%). This highlights the inconsistency of population trajectories within individual patches. Small populations that are either static or decreasing in size may suddenly begin explosive growth in response to environmental change, as illustrated by the following cases. Plot W5 had the heaviest shade and most saturated soils of the wetland plots. It showed very limited seedling recruitment and no seed production in 2003 and 2004. 2005 was a very dry year, with only 251 mm of precipitation during the growing season (average for the other years was 747 mm). Many of the patches declined with this drought. However, it reduced the waterlogged conditions of W5 enough to prompt a vigorous late germination flush of seeds still present in the seedbank from the initial sowing. These plants appeared too late to be detected in the early June recruitment count. By fall, however, they had produced thousands of seeds, and recruitment in spring 2006 (a fairly dry year) was quite high. Another example is a plot under intact forest canopy whose initially stagnant growth dramatically increased after a large branch fell and opened a light gap above it. R5 is a roadside patch whose population growth accelerated drastically partway through the experiment; this may have been caused by increased disturbance due to increased farm vehicle use of a side

track that branched off the main road adjacent to the plot. Despite the fact that this increased disturbance was not intense enough to expose the soil, there may have been enough impact on the established plant community to release *M. vimineum*.

The fact that *M. vimineum* was found in all surviving plots in all years (with the exception of the patches lost to *R. multiflora*) is especially remarkable in light of the review of seed introduction studies by Turnbull et al. (2000). They found that in published experiments censusing both seedlings and adults on sites where new species were sown, seedlings were found on 64% of the sites but adult plants in only 23%. Thus for many species plant establishment and survival are limiting stages of population growth, but this does not seem to be the case for *M. vimineum*. Rather, our results suggest that *M. vimineum* is capable of establishing in a wide variety of conditions; the “bottleneck” in its invasion cycle is seed dispersal. Indeed, there were only three plots in which *M. vimineum* dispersed more than 2 m from the original plots over the course of four years. Rauschert et al. (in press) model the spatial spread of *M. vimineum* and discuss its implications at a landscape scale.

Analysis of Environmental Variables

The environmental variables which best explained variation in population metrics were all related to soil characteristics and plant species richness (Table 1.3). The best model generated by best subsets regression for 2004 stem counts included only soil ammonium-N, negatively correlated with stem count (adj. R^2 is 27.4%). The model selected for 2004 seed production again includes a significant negative correlation with ammonium-N, as well as a non-significant positive correlation with soil pH (adj. $R^2 = 52.1\%$). According to Ehrenfeld et al. (2001), *M. vimineum* prefers nitrate-N to ammonium-N, which could explain the significant negative correlation with $\text{NH}_4\text{-N}$ in these models.

Model	Variable	Coefficient	Std. Coeff.	P	Model Adj. R^2
2004 stems	(Intercept)	6.220		<0.0001	27.4%
	Ammonium-N	-0.071		0.0051	
2004 seeds	(Intercept)	6.911		<0.0001	52.4%

	Ammonium-N	-0.169		<0.0001	
	pH	0.402		0.2464	
2006 stems	(Intercept)	-4.116	0	0.0104	73.3%
	Moisture	9.894	0.614	<0.0001	
	pH	1.154	0.509	0.0025	
	K	-0.017	-0.507	0.0101	
	P	0.034	0.420	0.0127	
	Plant spp. richness	0.170	0.318	0.0114	

Table 1.3. Multiple regression models for *M. vimineum* patch stem and seed counts, with predictor variables selected by best subsets algorithm. All response variables are log transformed. Std. Coeff is the regression coefficient when data have been standardized.

The environmental variables explained only a modest amount of the variation in 2004 recruitment, a count which reflects the condition of the populations after only one growing season. The improved model fit with the fecundity data likely reflects the fact that seed production integrates the effects of site throughout the entire growing season. That fit was even stronger in the 2006 data. Early in the experiment the populations were in the earliest stages of growth and had not had a chance to diverge much. As the experiment progressed through a number of growing seasons, populations diverged more as the impacts of environmental factors became more manifest.

The model generated for 2006 stems has quite good explanatory power, with an adj. R^2 of 73.3% (Table 1.3). This model includes five variables: soil moisture, pH, P, and K, and number of species in the surrounding plant community. The most important variable, both in statistical significance and magnitude of effect, was soil moisture (Figure 1.2). Seedling recruitment was higher in moister patches in this year, which was dry: the area received only 441 mm of precipitation during the growing season. This highlights how lack of adequate moisture can limit *Microstegium* recruitment; however, in the case of patch W5, recruitment was limited by excessive soil saturation.

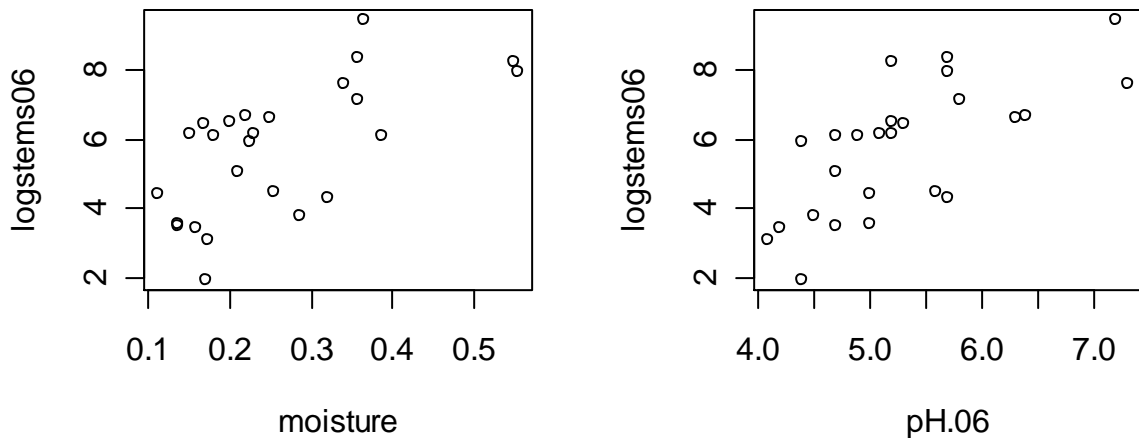


Figure 1.2. Relationship of 2006 seedling counts to (a) soil moisture and (b) pH.

The strong positive effect of pH in the 2006 model (Figure 1.2) is of particular interest as many forest disturbances elevate soil pH, such as limestone gravel use on forest roads (A. Nord, unpublished data) and liming the soil to revegetate logging roads (R. White, PA Bureau of Forestry District 5, pers. comm.) Previous work has shown *M. vimineum* presence was correlated with higher soil pH (Cole and Weltzin, 2004). It has also been reported that *M. vimineum* may raise soil pH (Ehrenfeld et al., 2001). Whether because the growth of the native flora is suppressed by elevated pH or that *M. vimineum* prefers higher soil pH, *M. vimineum* presence and population growth is favored in soils with high pH.

Another important variable in the 2006 model is the number of other plant species present in the plots. We found a positive correlation between seedling recruitment and species richness, consistent with a body of research suggesting that areas which support more diverse plant communities are more invasible (reviewed by Levine and D'Antonio, 1999). Note, however, that this relationship is debated in the literature (cf Byers and Noonburg, 2003; Tilman, 2006). The significant negative relationship with soil potassium is interesting in light of Barden's (1987) finding of a negative relationship between soil K and *M. vimineum* production of seed spikes.

Management Implications

This study demonstrates that we may not safely consider “stalled” invasions to be “failed.” Nor can we assume that the results of one-time surveys for invasive species are applicable across time, as populations of even the most invasive annual species may fluctuate from year to year. We must also realize that community resistance to invasions by *M. vimineum*, and probably other species as well, is not static. Our patch case studies illustrate how invasibility in these communities can change dramatically with very small-scale environmental changes: light gaps, soil moisture fluctuations, disturbance. While the limited size of our study prevents statistical inferences about such patterns, it is important to recognize the possibility that key environmental changes may trigger explosive growth in populations that appear to be static or even declining.

Our results cast doubt on the possibility of producing habitat-based risk assessment models for species such as *M. vimineum*, whose populations are largely controlled by factors that vary at too small a scale to be accurately mapped. This does not, however, negate the real need for risk assessment as a management tool. A more feasible approach may be to identify those environmental changes or disturbances which most stimulate population growth in the species of concern, the “switches” which can “turn on” population growth (especially disturbance and increased light availability), and identify which areas are most likely to experience such changes.

Sources of Materials

- ¹SONY DSC-P8 MPEG Movie VX, focal length 39 mm. Sony Corporation of America, New York, NY.
- ²Photoshop CS3 software, version 10.0.1, 2007. Adobe Systems Inc., San Jose, CA.
- ³Apogee Quantum Meter LQS 50-3M soil moisture probe. Apogee Instruments Inc., Roseville, CA.
- ⁴JMP statistical software, version 5.1, 2003. SAS Institute, Cary, NC.
- ⁵Minitab statistical software, version 14.0, 2002. Minitab Inc., State College, PA.
- ⁶R statistical and programming software, version 2.3.1, 2007. R Development Core Team.

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Literature Cited

- Barden, L.S. 1987. Invasion of *Microstegium vimineum* (Poaceae), an exotic, annual, shade-tolerant, C4 grass, into a North Carolina floodplain. *American Midland Naturalist* 118: 40-45.
- Braker, W.L. 1981. Soil Survey of Centre County, Pennsylvania. Washington, D.C.: USDA-SCS.
- Byers, D.L., Quinn, J.A. 1998. Demographic variation in *Alliaria petiolata* (Brassicaceae) in four contrasting habitats. *Journal of the Torrey Botanical Society* 125: 138-149.
- Byers, J.E., Noonburg, E.G. 2003. Scale dependent effects of biotic resistance to biological invasion. *Ecology* 84: 1428-1433.
- Christen, D.C., Matlack, G.R. 2009. The habitat and conduit functions of roads in the spread of three invasive plant species. *Biological Invasions* 11: 453-465.

- Cole, P.G., Weltzin, J.F. 2004. Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeastern Naturalist* 3: 545-562.
- Cole, P.G., Weltzin, J.F. 2005. Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. *Biological Invasions* 7: 477-488.
- Crooks, J.A., Soule, M.E. 1999. Lag times in population explosions of invasive species: Causes and implications. Pages 103-125 in O.T. Sandlund, P.J. Schei, A. Viken, eds. *Invasive Species and Biodiversity Management*. New York: Springer.
- Ehrenfeld, J.G., Kourtev, P., Huang, W. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11 (5) 1287-1300.
- Hunt, D.M., Zaremba, R.E. 1992. The northeastward spread of *Microstegium vimineum* (Poaceae) into New York and adjacent states. *Rhodora* 94 167-170.
- Jongejans, E.S., O; Tipping, PW; Shea, K. 2007. Establishment and spread of founding populations of an invasive thistle: the role of competition and seed limitation. *Biological Invasions* 9: 317-325.
- Kollmann, J., Frederiksen, L., Vestergaard, P., Bruun, H.H. 2007. Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biological Invasions* 9: 31-42.
- Koop, A.L. 2004. Differential seed mortality among habitats limits the distribution of the invasive non-native shrub *Ardisia elliptica*. *Plant Ecology* 172: 237-249.
- Levine, J.M., D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15-26.
- Li, Y. et al. 2004. Predicting super spreading events during the 2003 Severe Acute Respiratory Syndrome epidemics in Hong Kong and Singapore. *American Journal of Epidemiology* 160: 719-728.
- Marchetti, M.P., Moyle, P.B., Levine, R. 2004. Alien fishes in California watersheds: Characteristics of successful and failed invaders. *Ecological Applications* 14: 587-596.
- Marshall, J.M., Buckley, D.S. 2008. Influence of litter removal and mineral soil disturbance on the spread of an invasive grass in a Central Hardwood forest. *Biological Invasions* 10: 531-538.
- Meekins, J.F., McCarthy, B.C. 2001. Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecological Applications* 11: 1336-1348.
- Mehrhoff, L.J. 2000. Perennial *Microstegium vimineum* (Poaceae): An apparent misidentification? *Journal of the Torrey Botanical Society* 127: 251-254.
- Mortensen, D.A., Rauschert, E.S.J., Nord, A.N. 2009. Forest roads facilitate the spread of invasive plants. *Invasive Plant Science and Management In press*.

- Neter, J., Kutner, M.H., Nachtsheim, C.J., Wasserman, W. 1996. Applied Linear Statistical Models. 4th ed. Chicago, IL: Irwin. Pp. 1408.
- Oswalt, C.M., Clatterbuck, W.K., Oswalt, S.N., Houston, A.E., Schlarbaum, S.E. 2004. First-year effects of *Microstegium vimineum* and early growing season herbivory on planted high-quality oak (*Quercus* spp.) seedlings in Tennessee. Proceedings of the 14th Central Hardwoods Forest Conference: 1-9.
- Oswalt, C.M., Oswalt, S.N. 2007. Winter litter disturbance facilitates the spread of the nonnative invasive grass *Microstegium vimineum* (Trin.) A. Camus. Forest Ecology and Management 249: 199-203.
- Oswalt, C.M., Oswalt, S.N., Clatterbuck, W.K. 2007. Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. Forest Ecology and Management 242: 727-732.
- Peskin, N. 2005. Habitat suitability of Japanese Stiltgrass *Microstegium vimineum* in an Appalachian forest M.S.: The Pennsylvania State University.
- Quinn, G.P., Keough, M.J. 2002. Experimental Design and Data Analysis for Biologists Cambridge, UK: Cambridge University Press. Pp. 537.
- Radosevich, S.R., Holt, J.S., Ghersa, C.M. 2007. Ecology of Weeds and Invasive Plants: Relationship to agriculture and natural resource management. 3rd ed. Hoboken, New Jersey: John Wiley & Sons, Inc.
- Rauschert, E.S.J. 2010. Slow spread of the aggressive invader, *Microstegium vimineum* (Japanese stiltgrass). Biological Invasions 12:563-579.
- Redman, D.E. 1995. Distribution and habitat types for Nepal microstegium [*Microstegium vimineum* (Trin.) Camus] in Maryland and the District of Columbia Castanea 60: 270-275.
- Tanentzap, A.J., Bazely, D.R. 2009. Propagule pressure and resource availability determine plant community invasibility in a temperate forest understorey. Oikos 118: 300-308.
- Tilman, D. 2006. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455-1474.
- Tu, M. 2000. Element stewardship abstract for *Microstegium vimineum*: The Nature Conservancy.
- Turnbull, L.A., Crawley, M.J., Rees, M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88: 225-238.
- Winters, K., Schmitt, M.R., Edwards, G.E. 1982. *Microstegium vimineum*, a shade adapted C4 [carbon pathway] grass [Comparison of growth with *Digitaria sanguinalis* and *Sporobolus airoides*]. Plant Science Letters 24: 311-318.
- Wiser, S.K., Allen, R.B., Clinton, P.W., Platt, K.H. 1998. Community structure and forest invasion by an exotic herb over 23 years. Ecology 79: 2071-2081.

Chapter 2

Limestone gravel on unpaved roads increases abundance of invasive *Microstegium vimineum* (Japanese stiltgrass)

Abstract

It has been well established that the physical conditions associated with roads can foster the dispersal and establishment of invasive plants. However, the effects of road-related chemical changes on invasive plants have received less attention. Limestone gravel is frequently used to surface unpaved forest roads in Pennsylvania, where native soils are often acidic and derived from shale. I surveyed roads surfaced with limestone and roads surfaced with shale to determine the effect of limestone gravel on pH of adjacent soils. I also quantified the abundance and distribution of *Microstegium vimineum* (Japanese stiltgrass), a problematic invasive commonly found along forest roads in the eastern US. I found that the pH of the upper 5 cm of soil near to limestone roads was significantly elevated. At the edge of shale roads soil pH was 5.5; at 5 m from the edge, pH was not significantly different from that at 25 m (3.70 ± 0.08). Soil pH was 7.83 ± 0.08 at the edge of the limestone roads and 4.58 ± 0.21 at 25 m. *M. vimineum* mean total abundance in the limestone roadside plant communities ($35.1 \pm 5.4\%$) was significantly greater than along shale roads ($11.5 \pm 2.2\%$). Mean extent of *M. vimineum* away from the road edge, was also greater on limestone roads (7.6 ± 0.22 m) than shale roads (2.55 ± 0.93 m). In a greenhouse trial, optimum *M. vimineum* growth occurred at pH 6.1, a pH higher than that measured along shale roads. I conclude that use of limestone gravel on unpaved forest roads results increases abundance of *M. vimineum*.

Introduction

That roads play an important role in plant invasions has been well established (Forman and Alexander 1998, Trombulak and Frissell 2000, Mortensen et al. 2009). They can act as corridors, providing connectivity within landscapes and facilitating

movement of humans and vehicles which disperse propagules (Tyser and Worley 1992, Von der Lippe and Kowarik 2007, Mortensen et al. 2009). Furthermore, the physical environment created by the presence of roads, particularly increased disturbance and light availability, is itself conducive to the establishment and growth of many invasive plants (Parendes and Jones 2000, Watkins et al. 2003).

The presence of roads can impact the chemical environment as well. Much of this work has focused on the effects of heavy metals from gasoline additives, deicing salts, and ozone and nitrogen from vehicle exhaust (Trombulak and Frissell 2000). These impacts are obviously most profound near major, heavily-trafficked roads. Little work has addressed the chemical impact of minor, unpaved roads, despite the fact that the extent of unpaved roads is quite large. There are over 40,000 km of unpaved roads in Pennsylvania (PA Dept of Ag 2010) and over 2.5 million km throughout the US (AASHTO 2010); much of this distance in Pennsylvania is through less developed areas such as forests and natural areas. Moreover, the network of unpaved roads is likely to expand considerably in the near future with the rapid rise in natural gas extraction (Penn State Marcellus Center for Outreach and Research, pers. comm.). Limestone gravel (usually dolomitic limestone) is often used to surface these roads, as it provides a resistant, durable driving surface (J. Lipko, Pennsylvania Bureau of Forestry, pers. comm.). While forest soils are generally acidic (Brady and Weil 2002), when limestone gravel is used to surface unpaved forest roads the pH of nearby soils can be raised to over 7 (K. Butler unpublished data). Thus any impact from limestone road dust is potentially both spatially extensive and ecologically significant.

Deposition of limestone dust and the accompanying changes in soil chemistry can lead to shifts in plant communities. Shifts in species presence and/or abundance have been documented in a variety of systems: Arctic tundra, in response to calcareous dust from a gravel road (Auerbach et al. 1997); oak forest in Virginia (U.S.) near limestone processing plants; and British heathlands near limestone quarries (Farmer 1993). Naturally higher soil pH has been shown to be correlated with higher survival of Norway maple (*Acer platanoides*) seedlings in the northeastern US (Martin and Marks 2006) and with increased presence of non-

aggressive exotic species in Quebec (Gilbert and Lechowicz 2005). However, to date no studies have addressed the question of whether changes in soil pH caused by limestone dust deposition can make plant communities more vulnerable to invasion by exotic species.

Microstegium vimineum is an invasive annual grass found in a wide variety of habitats throughout the eastern United States (Redman 1995). Its presence along roads has been well documented (Cole and Weltzin 2004, Mortensen et al. 2009). Several characteristics of the roadside environment favor its growth and spread. It benefits from disturbance (Oswalt and Oswalt 2007, Marshall and Buckley 2008) and the increased light from canopy openings (Christen and Matlack 2009). Its seeds easily move with water (Mehrhoff 2000), so the ditches and surface flow associated with roads act as dispersal agents. It may also be spread by the activities of road maintenance, such as grading (Mortensen et al. 2009).

Evidence suggests that *M. vimineum* prefers soils which are not strongly acidic. A field survey in Tennessee forests found its presence to be correlated with higher pH (Cole and Weltzin 2004). Higher soil pH was one of the most significant environmental factors correlated with greater population growth of experimentally planted patches in central Pennsylvania (Nord et al. 2010). It has also been reported that *M. vimineum* can raise the pH of soil in which it grows (Ehrenfeld et al. 2001). However, the question of whether *M. vimineum* is more invasive in less acidic soils has not been tested.

My objective in this study was to determine if the presence or abundance of *Microstegium vimineum* along unpaved forest roads is correlated with the changes in soil chemistry induced by the presence of limestone gravel on the road surface. I hypothesized that (1) the pH of soil along the roads would be significantly raised by the presence of limestone gravel; (2) *M. vimineum* would be more abundant on limestone than on native shale roads; and (3) *M. vimineum* would be found at greater distances from the edge of limestone roads than shale roads.

Methods

Study sites

Both Rothrock State Forest and Bald Eagle State Forest are located in the ridge and valley topographic province of central Pennsylvania. Second-growth oak-hickory forest is the dominant vegetation type. All study sites were situated on ridge slopes, where soils are largely of the Hazleton-Laidig-Andover association (Braker 1981) and are acidic, with average pH at the surface about 4.0 (Higbee 1967).



Figure 2.1. Locations of road pairs in A) Rothrock State Forest and B) Bald Eagle State Forest. Solid lines represent limestone gravel roads; dashed lines represent shale gravel roads. Each marked line segment is 1 km long.

Four pairs of unpaved roads in state forests were chosen, one in Rothrock State Forest and three in Bald Eagle State Forest (Figure 2.1). Each pair consisted of one road with limestone gravel and one surfaced with native shale. In two pairs, the two roads intersected; in the other two, they were selected to be as close together as

possible (within 0.5 km) and of comparable landscape position. The limestone gravel on the roads had been present for at least 15 years. In Bald Eagle State Forest, all the roads had initially been shale gravel but approximately 15 years before the study certain roads were selected to be surfaced with limestone as part of a project to improve roads designated as part of a snowmobile loop. When State Forest personnel first began to notice increased *M. vimineum* invasion along the roads recently graveled with limestone they visited the quarry from which their limestone gravel was obtained and ascertained that the gravel was not contaminated with *M. vimineum* propagules (J. Lipko, pers. comm.). Maintenance regimes (mowing roadside vegetation, grading, and blowing leaves out of the ditches) were the same within all road pairs.

Soil Sampling

In October 2009, data were collected to characterize the pH profile of the road pairs. Along each 1000-m road section, transects were laid perpendicular to the roadway at approximately 200, 400, 600, and 800 m. At each of the four transects and on either side of the road, soil samples were collected from the top 5 cm of soil at 0, 1, 2, 3, 5, 10, and 25 m from the edge of the road. In October 2010, additional samples were collected from limestone roads at 25 and 40 m distances.

Soil samples were oven-dried at 110° C to constant weight. After passing through a 2-mm screen, they were made into a 2:1 slurry with deionized water and measured for pH with an Orion 525A+ benchtop pH meter (Thermo Electron Corp., Beverly, MA).

Field Survey: *M. vimineum* abundance

Road pairs were surveyed for *M. vimineum* presence and abundance in July 2009. Five categories were established for the visual assessment of *M. vimineum* abundance: absent; sparse (*M. vimineum* consisted of less than 10% of the roadside vegetation); low (between 10 and 40%); medium (between 40 and 70%); and high (over 70%). A distance wheel was used to measure 1000 m from the starting point on both the upslope and downslope sides of each road. The width of the area surveyed was the strip between the road proper and the forest vegetation, which was generally

between 1.5 and 2.5 m wide. Abundance category of the *M. vimineum* present in this strip of roadside vegetation was continually assessed as the 1000 m sections were measured, with distance measures at category transitions recorded. In the left panel of Figure 2.2, the arrows represent each category segment measured. For intersecting road pairs, the wheel was started at least 20 m from the intersection. Portions of roadside consisting of anomalies such as driveways, parking turnouts, or culvert washes were excluded from the assessment.

This survey was repeated on two of the road pairs in July 2010 (the one in Rothrock SF and one in Bald Eagle SF). The remaining two pairs could not be surveyed because of mowing and herbicide application to the roadside vegetation.

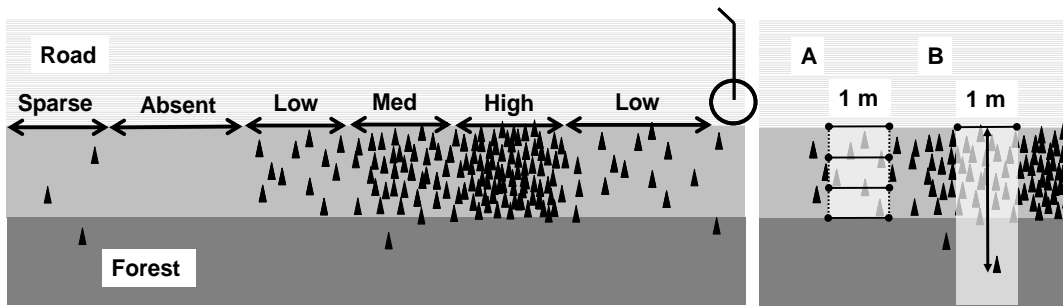


Figure 2.2. Left: Schematic representation of field survey for abundance of *M. vimineum* (represented by black triangles) in roadside vegetation. Right: A) positioning of quadrats and B) measurement of *M. vimineum* extent away from roadside.

Field Survey: Quadrats

For each side of each road in 2009, three points in each abundance class were randomly selected for placement of quadrats. As not all abundance classes were found on all roads, and as I determined that sections of road in a given abundance category must be at least 2 m in length to place a quadrat, I placed 206 quadrats on limestone roadsides and 109 on shale. For the quadrats, a 1-m wide sampling device with extending rope sides was positioned, with one side at the boundary between road and vegetation, and the rope sides extending the sample area to the boundary between roadside and forest interior vegetation. To make visual estimation of percent cover

more accurate, 1-m lengths of PVC divided the sample area into 1 x 0.5 m subunits (Figure 2.2A). Within each subunit, percent cover of *M. vimineum*, other graminoids (grasses and sedges), dicots, ferns, and bare ground was estimated. The furthest extent of *M. vimineum* away from the road within this 1-m width was measured (Figure 2.2B).

A digital photograph of the forest canopy directly above the sample area was taken with a Pentax digital K100 camera with an 18-mm lens, leveled 0.5 m above the ground. These images were processed with the GNU Image Manipulation Program (GIMP Development Team 2008) to determine percent canopy cover.

In July 2010, in order to test independence of opposite road sides with respect to *M. vimineum* abundance, I sampled *M. vimineum* percent cover at points directly across the road from each other at ten evenly-spaced locations on each road pair surveyed that year, using the 1-m wide sampling device.

Mycorrhizal Sampling

In September 2009, roots from twelve *M. vimineum* plants were composited from each road type in Rothrock State Forest and preserved in 50% ethanol. These were stained with trypan blue and the presence of arbuscular mycorrhizae was quantified with the line intersect method (Koide and Mooney 1987)

Foliar Tissue Analysis

In August 2010, before anthesis, *M. vimineum* plants were collected from the road pair in Rothrock State Forest. Plants were taken from within 1 m of the road edge over several hundred meters of road length, from both the shale and limestone road. Stems were removed; the leaves were dried at 55°C and sent to The Pennsylvania State University Agricultural Analytical Lab for combustion analysis of total nitrogen, and acid digestion and ICP emission spectroscopy analysis of other major elements.

Greenhouse Experiment

In fall 2008, *M. vimineum* seed was collected from several sites in Rothrock State Forest. The seed was pooled and stored at room temperature. Clarksburg loam

soil from a nearby forest site was collected from the upper 5 cm of soil. The soil was dried for 4 days at 58 ° C to kill the seed bank and the mycorrhizal community.

In February 2009, soil was amended with powdered dolomitic limestone to achieve three elevated pH treatments (6.1, 7.2, and 8.3) in addition to the unamended treatment (pH 5.0). Soil for all treatments was moistened and incubated 5 weeks in the greenhouse, stirred weekly, then used to fill 21 cm deep cone-tainers (164 ml volume; Steuwe & Sons, Tangent, OR). *M. vimineum* was planted in March 2009 in 25 replicates of each treatment. Cone-tainers were completely randomized, and re-randomized weekly throughout the experiment. Six weeks after planting, all above-ground biomass was harvested, oven-dried to constant weight, and weighed.

Statistical Analysis

All statistical tests were performed with R, version 2.9.2 (R Development Core Team 2009). Maximum likelihood mixed-effects models were done with the R package nlme (Pinheiro et al. 2009). Significance was identified at $\alpha = 0.05$.

First I used ANOVA to test whether there were significant differences in canopy openness between limestone and shale treatments in the surveyed roads. I used canopy cover from the digital photographs as the response variable with road type as factor. I also used a linear model to test whether canopy openness above the quadrats was a good predictor of *M. vimineum* density measured within the quadrats.

I tested the independence of upslope and downslope sides of each roads with the percent cover data collected from opposite sides of the road in 2010, using R to calculate the correlation coefficient for each pair of road sides.

Within each side of each road, I summed the distance measured within each abundance category. Overall abundance was determined by multiplying the midpoint of the abundance category (0, 5%, 25%, 55%, and 85%) by the total distance measured on the roadside in that category. These products were then summed to determine average *M. vimineum* abundance for each road side. Average abundance was then used as a response variable in a mixed-effects ANOVA with road type as a fixed factor and road pair as a random factor.

To test for differences in extent of *M. vimineum* away from the road, I used the maximum distances from the road edge that *M. vimineum* was detected as a

response variable with road type and road side (upslope/downslope) as fixed factors and road pair as a random factor.

Results

Soil sampling

Soil pH in the upper 5 cm of soil along transects perpendicular to limestone roads was strikingly different from that of shale road transects (Figure 2.3). Along shale roads, pH at the edge of the road averaged 5.44 ± 0.10 (mean across both sides \pm s.e.); at the edge of limestone roads average pH was 7.83 ± 0.08 . On shale roads pH declined quickly with increasing distance from the road edge; pH at 5 m did not differ from that at 25 m, 3.70 ± 0.08 . The pH from limestone road transects declined much more slowly with distance from the road. At 25 m away from the road edge, the pH of the limestone road samples (4.58 ± 0.21) was still significantly higher than that of the shale road (3.70 ± 0.07). There was no difference in pH between 40 m samples from limestone roads and shale samples from 5, 10, or 25 m. At no distance was side (upslope or downslope) or the interaction of side and treatment significant.

Greenhouse experiment

Maximum growth of *M. vimineum* occurred in the pH 6.1 treatment (Figure 2.4). The least growth occurred in the highest pH treatment. Analysis of variance shows the treatment effect is highly significant (df=3, sum sq.=11.02, mean sq. =3.67, $F = 129.25$, $p < 0.0001$).

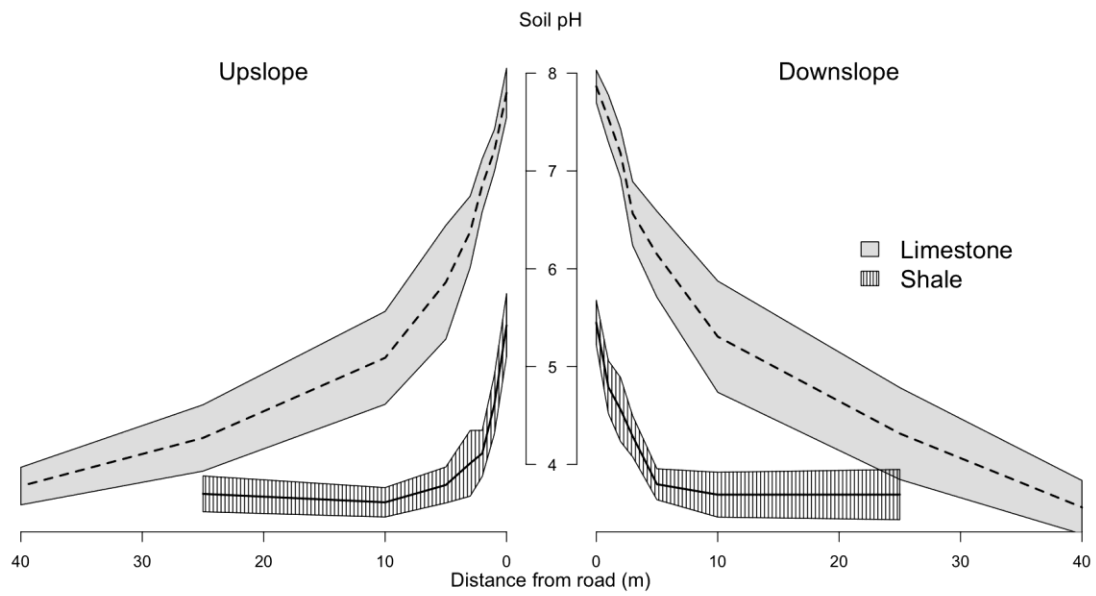


Figure 2.3. Soil pH (\pm 95% confidence interval) of samples taken from the top 5 cm at 0, 1, 2, 3, 5, 10, 25 and 40 m along transects laid perpendicular to limestone and shale roads, on both upslope and downslope sides.

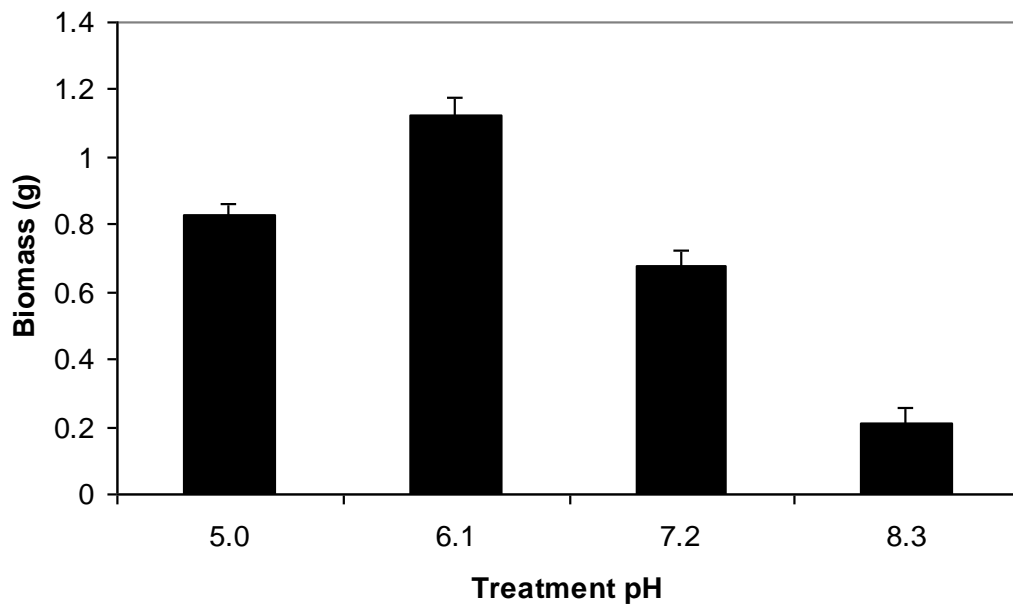


Figure 2.4. Above-ground biomass accumulation (means \pm SE) of *M. vimineum* after 6 weeks in four soil pH treatments.

Correlation of *M. vimineum* cover with upslope and downslope landscape positions

Percent cover of *M. vimineum* measured in the 2010 quadrats was not correlated with *M. vimineum* cover in the quadrats placed directly across the road in any of the four roads sampled. The absolute values of the correlation coefficients ranged from 0.07 to 0.52 with p-values between 0.12 and 0.85, and there were no consistent patterns of positive or negative relationships between upslope and downslope quadrats. Therefore upslope and downslope sides of each road are considered to be independent in my analyses.

Microstegium abundance

There was a marked difference between road types in the occurrence of *M. vimineum* abundance categories. About 70% of the shale roadside had scattered or no *M. vimineum*, while limestone roads had significantly greater distances measured in the higher abundance classes (Figure 2.5).

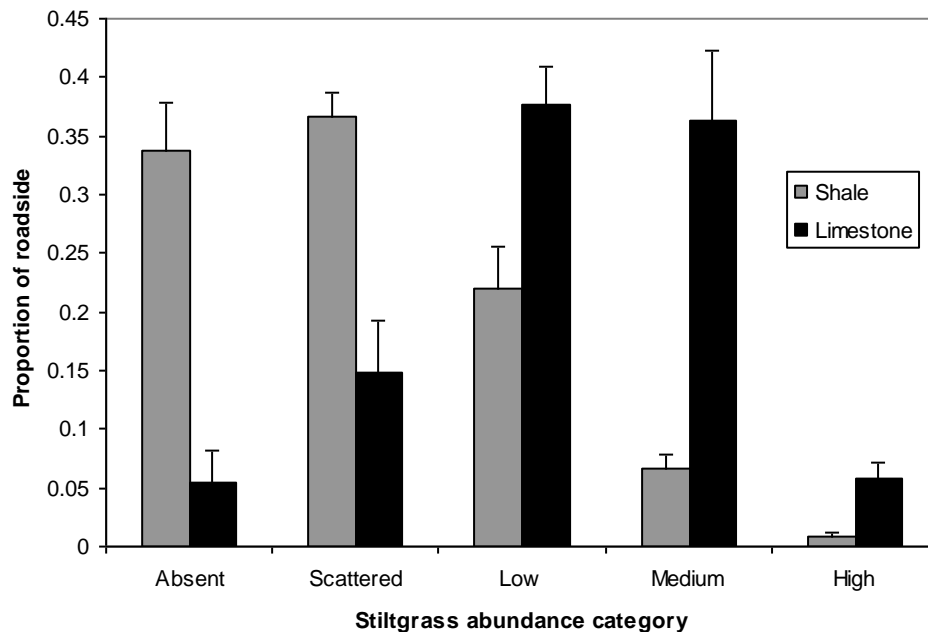


Figure 2.5. Proportion of roadside occurring in each *M. vimineum* abundance category (means \pm SE) along shale and limestone graveled roads.

Analysis of variance of the calculated abundance estimates for each road side, with road type as a fixed factor and road pair as random, confirms that differences in abundance between limestone and shale roads are significant but the effects of side (upslope or downslope) are not, nor is the interaction significant (Table 2.1).

	Num DF	Den DF	F-value	p-value
(Intercept)	1	9	22.70699	0.001
Road type	1	9	27.593283	0.0005
Side	1	9	0.10577	0.7524
Type:Side	1	9	0.643735	0.443

Table 2.1. Analysis of variance for test of difference in total *M. vimineum* abundance between road types (shale/limestone) and road sides (upslope/downslope).

The mean calculated average abundance of *M. vimineum* along limestone roads was more than three times higher than that of shale roads in both years (Figure 2.6). Along limestone roads, an average of 35.1% of the roadside area was covered by *M. vimineum* in 2009 and 37.1% in 2010; only 11.5% of shale roadsides area was covered by *M. vimineum* in both years.

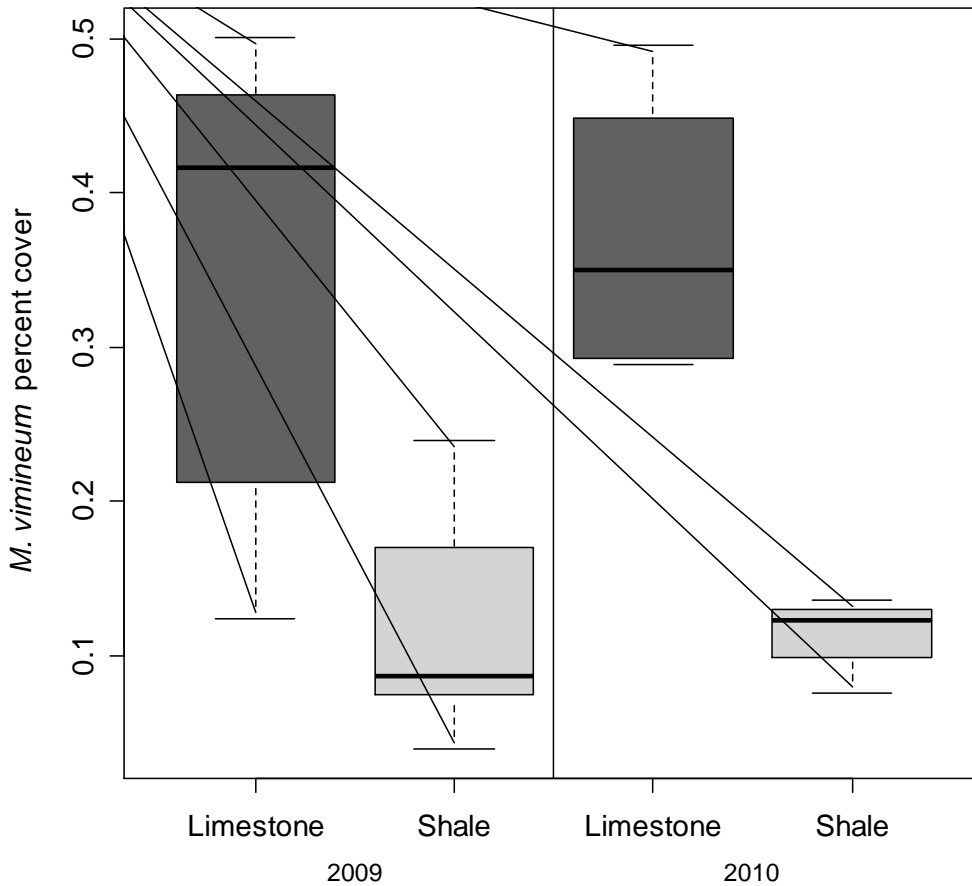


Figure 2.6. Boxplot of abundance estimates of *M. vimineum* (in percent cover) for the eight 1000-m road sections of each road type surveyed in 2009 and the four sections of each type surveyed in 2010. Dark lines show medians and shaded boxes show interquartile ranges (25th and 75th quartiles).

Microstegium extent

M. vimineum extent away from the road was significantly greater along limestone roads (7.6 ± 0.93 m) than shale roads (2.55 ± 0.22 m; $F=141.2$, $p<0.001$; Figure 2.7). In the ANOVA model, the term for side of road (upslope or downslope) was not significant, nor was the interaction of side and road type. The density of *M. vimineum* in a roadside quadrat was not a strong predictor of the extent of *M. vimineum* extent away from the road at that point (adj. $R^2 = 0.345$).

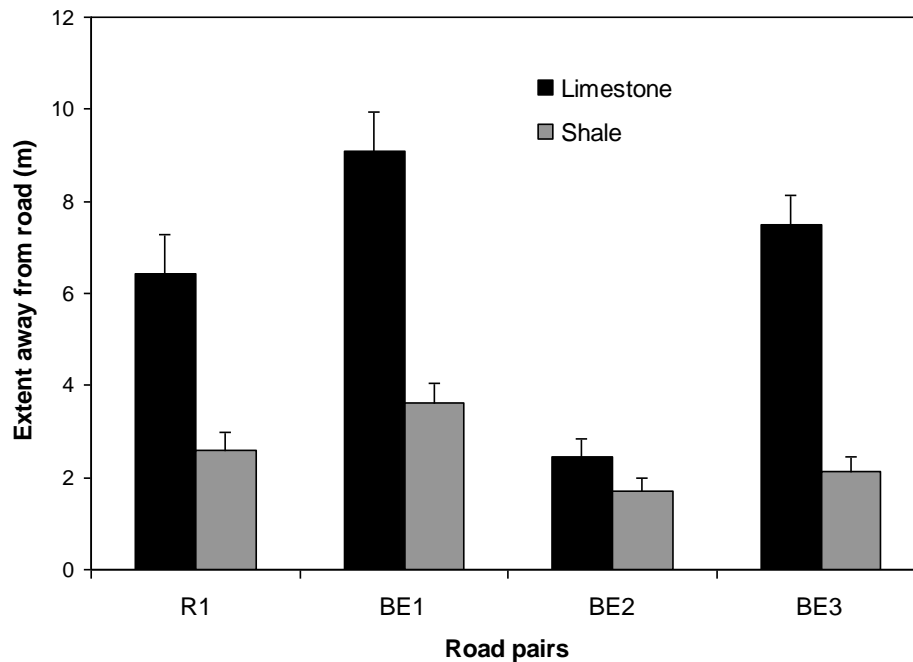


Figure 2.7. Furthest extent of *M. vimineum* away from edge of unpaved forest roads within width of 1 m quadrats on limestone and shale gravel roads (means \pm SE). Road pair designated with R is in Rothrock State Forest; those designated BE are in Bald Eagle State Forest.

Canopy openness

Mean canopy openness above the quadrats was $25.1 \pm 1.1\%$; analysis of variance showed no significant difference in canopy openness between limestone and shale roads. Therefore, my analysis of road surface treatment is not confounded by treatment differences in canopy openness. Canopy openness was not a good predictor of *M. vimineum* density in the quadrats from which the canopy images were taken ($p = 0.180$, adj. r-squared = 0.4%).

Other vegetation

There was no difference in cover of non-*M. vimineum* vegetation between shale and limestone roads ($F = 0.63265$, $p = 0.4273$). There was significantly more bare ground in the quadrats on shale roadsides ($49.6 \pm 2.7\%$) than along limestone ($37.2 \pm 2.5\%$; $F=13.009$, $p<0.0001$).

M. vimineum percent cover was not significantly correlated, either positively or negatively, with cover of any other vegetation type: other graminoids, dicots, or ferns.

Foliar Analysis

The most remarkable differences in foliar mineral content are in those elements whose availability to plants changes with soil pH. Mn, Fe, and Al concentrations are much higher in the plants from the shale road (Table 2.2). Ca content is much higher in plants from the limestone roads.

	Percent						Parts per million						
	N	P	K	Ca	Mg	S	Mn	Fe	Cu	B	Al	Zn	Na
Shale	2.97	0.37	1.31	0.80	0.31	0.25	155	340	27	10	138	30	101
Limestone	2.19	0.29	1.04	1.46	0.32	0.33	39	160	36	<10	75	27	99

Table 2.2. Foliar analysis of *M. vimineum* from shale and limestone road in Rothrock State Forest.

Mycorrhizal sampling

Examination of *M. vimineum* roots with the line intersect method showed very similar rates of mycorrhizal infection for both road types: 63% for limestone and 65% for shale. However, the mycorrhizal structures observed in roots from the two road types differed visually, with fewer but larger vesicles seen in roots from the shale environment.

Discussion

The results of this study provide several lines of evidence that use of limestone gravel on forest roads in central Pennsylvania increases the vulnerability of roadside plant communities to invasion by *M. vimineum*.

The differences in soil pH between shale road corridors and limestone road corridors were striking. The pH of the upper 5 cm is somewhat higher than that of undisturbed forest soils even beside shale roads, as road side soils in general contain much less organic matter which is acidic. However, the pH along limestone roads was elevated to the point of alkalinity in the first 1 m from the road edge, and was still higher than that of comparable shale road soils 25 m away from the road's edge. This represents a considerable area of forest affected by limestone dust: for every 1 km of road, at least 5 ha of roadside and forest vegetation experience elevated pH. This may represent an ecologically significant disturbance in a forest whose soils are naturally quite acidic.

Limestone roads were more heavily invaded by *M. vimineum* than shale roads in every road pair surveyed. Furthermore, *M. vimineum* extends further away from the edges of these roads into the forest. The greatest soil pH effect from the limestone is within the first 10 m from the road edge. The means of *M. vimineum* extent away from the limestone road edge were all within 10 m as well (Figure 2.7). This suggests a causal relationship between the elevated pH and the extent of *M. vimineum* away from the road.

One possible explanation for the increased susceptibility of limestone roadside communities to *M. vimineum* invasion is that the altered soil chemistry inhibits the rest of the roadside plant community which might be more acidophilic, leaving open resources and less competition for *M. vimineum*. However, we see that this is not the case: the data from the 2009 quadrats on all four road pairs show there is no significant difference in amount of non-*M. vimineum* vegetation between shale and limestone roads. While there is significantly more *M. vimineum* cover in plant communities beside limestone roads, there is significantly more bare ground beside shale roads. This suggests that the altered soil chemistry presents an opportunity that *M. vimineum* is uniquely able to exploit.

In the greenhouse experiment, optimum growth of *M. vimineum* occurred at pH 6.1. This is well within the range measured within the first two m from limestone road edges, but is higher than that from the shale roads. The poor performance of *M. vimineum* at extremely high pH was surprising in light of my observations of vigorous growth in the field at that pH. However, I had heated the soil sufficiently to kill most if not all mycorrhizal propagules. *M. vimineum*, like most other C4 grasses, associate with arbuscular mycorrhizae in the field. Mycorrhizae are especially beneficial to their host plants in the acquisition of phosphorus, a nutrient which is less available to plants at high soil pH. Therefore it is very likely that *M. vimineum* is dependent on mycorrhizal associations in the high pH conditions of the limestone roadside communities. Arbuscular mycorrhizal (AM) species have fairly narrow environmental tolerances to variables such as soil pH (Porter et al. 1987b, a), and it is unlikely that the AM species *M. vimineum* would encounter in the more acidic soils along shale roads would be the same as those encountered in the much less acidic soils along limestone roads. This is consistent with my observations of morphological differences in arbuscular mycorrhizae infecting the roots of *M. vimineum* collected from the two road types. It is possible that *M. vimineum* benefits more from the AM community present in the limestone roadside environment than from that present in the shale environment; different species of AM fungi can differ in the extent of benefit conferred on the host, and the same AM species can vary in its contribution to its host depending on factors such as soil pH (Hayman and Tavares 1985).

Another possibility is that *M. vimineum* is sensitive to an excess of available aluminum and/or manganese in the soil. Aluminum is less available to plants at higher soil pH, but can limit plant growth in soils of less than 5.0 (Marschner 1995, Rout et al. 2001). Manganese is necessary for plant growth but in excess can be toxic, and it is more available to plants when soil is acidic (Marschner 1995) thus its effect would be negligible on plants growing within 10 m of limestone roads, where average pH is high enough that very little aluminum or manganese would be available. However, at one m from shale road edges the average pH has declined to 4.8; thus most of the soil in this roadside plant community is acidic enough to cause

aluminum toxicity problems in sensitive plants. The foliar analyses show that the leaves of *M. vimineum* from shale roadsides contain much more aluminum and manganese than those from limestone roadsides, suggesting that *M. vimineum* is not well able to limit aluminum uptake. If aluminum- or manganese- stressed *M. vimineum* plants on acidic shale roadsides produce less seed than plants in less acidic limestone roadsides, this could explain the differences in abundance that I observed.

This work is an important addition to the existing body of literature on the role of roads in plant invasions. Limestone use as a road surface dramatically increases soil pH, which in turn is correlated with the distribution and abundance of an aggressive invasive. While it is well-documented that disturbances such as timber harvest, soil movement, and fragmentation can facilitate the establishment of invasive plants (e.g. Brothers and Spingarn 1992, Silveri et al. 2001, Hansen and Clevenger 2005, Fleishman et al. 2006), changes in soil chemistry have received much less attention in the literature (Trombulak and Frissell 2000). These results call for recognition that dust deposition from forest roads surfaced with limestone gravel is an anthropogenic perturbation which can have profound impacts on surrounding plant communities in the dust deposition corridor. The increased susceptibility to invasion of *M. vimineum* is one such impact easily seen in the short term. These communities may also prove more susceptible to other invasive species which prefer less acidic conditions, such as honeysuckles (*Lonicera* spp.) (Schierenbeck 2004) or invasive earthworms (Tiunov et al. 2006). Other community-level effects might not become apparent until much later. For example, at present much of the understory vegetation consists of acidophilic ericaceous shrubs. There could be significant shifts in understory composition in the road corridors in the future if the elevated pH in the upper few cm of soil prevents germination of seeds of species which require acidic conditions.

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Literature Cited

- AASHTO (American Association of State Highway and Transportation Officials) Center for Environmental Excellence website, accessed 3-11-10
http://environment.transportation.org/environmental_issues/construct_maint_prac/compendium/manual/5_8.aspx
- Auerbach, N. A., M. D. Walker, and D. A. Walker. 1997. Effects of roadside disturbance on substrate and vegetation properties in arctic tundra. *Ecological Applications* 7:218-235.
- Brady, N. C., and R. R. Weil. 2002. *The Nature and Properties of Soils*. 13th edition. Prentice Hall, Upper Saddle River, NJ.
- Braker, WL. 1981. *Soil Survey of Centre County, Pennsylvania* Washington, D.C. : USDA-SCS.
- Brothers, T. S. and A. Spingarn 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* 6:91-100.
- Christen, D. C., and G. R. Matlack. 2009. The habitat and conduit functions of roads in the spread of three invasive plant species. *Biological Invasions* 11:453-465.
- Cole, P. G., and J. F. Weltzin. 2004. Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeastern Naturalist* 3:545-562.
- Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11 (5) 1287-1300.
- Farmer, A. M. 1993. The Effects of Dust on Vegetation - a Review. *Environmental Pollution* 79:63-75.
- Fleishman, E., D. D. Murphy, and D.W. Sada. 2006. Effects of environmental heterogeneity and disturbance on the native and non-native flora of desert springs. *Biological Invasions* 8:1091-1101.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207-231.

- Gilbert, G., and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. *Ecology* 86:1848-1855.
- Hansen, M. J. and A. P. Clevenger. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological Conservation* 125:249-259.
- Hayman, D. S., and M. Tavares. 1985. Plant-Growth Responses to Vesicular-Arbuscular Mycorrhiza .15. Influence of Soil-Ph on the Symbiotic Efficiency of Different Endophytes. *New Phytologist* 100:367-377.
- Higbee, H.W. 1967. Land Resource Map of Pennsylvania. The Pennsylvania State University Department of Agronomy, University Park, PA.
- Kimball S, Mattis P, and the GIMP Development Team. 2008. GIMP: GNU image manipulation program. Available at <http://www.gimp.org>.
- Koide, R. T., and H. A. Mooney. 1987. Spatial variation in inoculum potential of vesicular-arbuscular mycorrhizal fungi cause by formation of gopher mounds. *New Phytologist* 107:173-182.
- Marschner, H. 1995. Mineral Nutrition of Higher Plants. 2nd ed. edition. Academic Press, Inc., San Diego, CA.
- Marshall, J. M., and D. S. Buckley. 2008. Influence of litter removal and mineral soil disturbance on the spread of an invasive grass in a Central Hardwood forest. *Biological Invasions* 10:531-538.
- Martin, P. H., and P. L. Marks. 2006. Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). *Journal of Ecology* 94:1070-1079.
- Mehrhoff, L. J. 2000. Perennial *Microstegium vimineum* (Poaceae): An apparent misidentification? *Journal of the Torrey Botanical Society* 127:251-254.
- Mortensen, D. A., E. S. J. Rauschert, A. N. Nord, and B. P. Jones. 2009. Forest roads facilitate the spread of invasive plants. *Invasive Plant Science and Management* 2:191-199.
- Nord, A. N., D. A. Mortensen, and E. J. S. Rauschert. 2010. Environmental factors influence early population growth of *Microstegium vimineum* (Japanese stiltgrass). *Invasive Plant Science and Management* 3:17-25.
- Oswalt, C. M., and S. N. Oswalt. 2007. Winter litter disturbance facilitates the spread of the nonnative invasive grass *Microstegium vimineum* (Trin.) A. Camus. *Forest Ecology and Management* 249:199-203.
- Parendes, L. A., and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conservation Biology* 14:64-75.
- Pennsylvania Department of Agriculture Dirt and Gravel Road Maintenance Program website, accessed 3-11-10.
http://www.agriculture.state.pa.us/portal/server.pt/gateway/PTARGS_0_2_24476_10

297_0_43/AgWebsite/ProgramDetail.aspx?name=Dirt-and-Gravel-Road-Maintenance-Program-%28DGRMP%29&navid=12&parentnavid=0&palid=25&

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and the R Core team (2009). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-93.

Porter, W. M., A. D. Robson, and L. K. Abbott. 1987a. Factors Controlling the Distribution of Vesicular Arbuscular Mycorrhizal Fungi in Relation to Soil-Ph. *Journal of Applied Ecology* 24:663-672.

Porter, W. M., A. D. Robson, and L. K. Abbott. 1987b. Field Survey of the Distribution of Vesicular Arbuscular Mycorrhizal Fungi in Relation to Soil-Ph. *Journal of Applied Ecology* 24:659-662.

R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.

Redman, D. E. 1995. Distribution and habitat types for Nepal microstegium [*Microstegium vimineum* (Trin.) Camus] in Maryland and the District of Columbia *Castanea* 60:270-275.

Rout, G. R., S. Samantaray, and P. Das. 2001. Aluminium toxicity in plants: a review. *Agronomie* 21:3-21.

Schierenbeck, K. A. 2004. Japanese Honeysuckle (*Lonicera japonica*) as an invasive species: history, ecology, and context. *Critical Reviews in Plant Sciences* 23:391–400.

Silveri, A., P. W. Dunwiddie, and H.J. Michaels. 2001. Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. *Biological Invasions* 3:379-389.

Tiunov, A. V., C. M. Hale, A. R. Holdsworth, and T. S. Vsevolodova-Perel. 2006. Invasion patterns of Lumbricidae into the previously earthworm-free areas of northeastern Europe and the western Great Lakes region of North America. *Biological Invasions* 8:1223-1234.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.

Tyser, R. W., and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). *Conservation Biology* 6:253-262.

Von der Lippe, M., and I. Kowarik. 2007. Long-Distance Dispersal of Plants by Vehicles as a Driver of Plant Invasions. *Conservation Biology* 21:986-996.

Watkins, R. Z., J. Q. Chen, J. Pickens, and K. D. Brososfske. 2003. Effects of forest roads on understory plants in a managed hardwood landscape. *Conservation Biology* 17:411-419.

Chapter 3

Effects of Environment and Suppression Method on *Microstegium vimineum* (Japanese Stiltgrass) Populations and Plant Communities

Abstract

Management aimed at suppressing invasive plants must take into account not only the efficacy of control techniques against target populations but also impacts on the non-target plant community. As many invasive plants occur across a wide range of environments, it is also important to consider site-specific efficacy and impacts of management techniques. I used herbicide and mechanical (string trimming) treatments in three environments commonly invaded by the annual grass *Microstegium vimineum*: along unpaved forest roads, upland forests 5-7 years after timber harvest, and wetlands. Herbicide used in logged and roadside environments was the grass-specific sethoxydim (Poast); in wetlands, an aquatic formulation of glyphosate (Rodeo) was applied. I monitored both *M. vimineum* populations and the non-target plant community for three years following the initial suppression treatments. Herbicides tended to suppress *M. vimineum* populations more than string trimming, although most differences were not statistically significant due to the variability of the data. Seed production was almost entirely prevented with herbicide but not with mechanical treatment. Bare ground, and thus opportunity for re-invasion, increased most when herbicide was applied in the wetland plots. Species richness of the non-target plant community increased more with mechanical treatment, particularly in the wetland environment. Changes in floristic quality tended to be more negative in the wetland chemical plots as well. I conclude that the “best” management option for *M. vimineum* varies by site. Selective herbicide in upland environments did little damage to non-target plant communities while adequately suppressing the invasive, but mechanical techniques were preferable in the wetland environment where the best permissible herbicide also suppresses the non-target plant community.

Introduction

Invasive plants present an increasing problem for forest managers. Competition from invasive plants can reduce native plant diversity (Hejda et al. 2009; 2004) and impede forest regeneration following disturbances such as timber harvest (Oswalt et al. 2007; Silveri et al. 2001). Plant invasions can impact other trophic levels (Baiser et al. 2008; Lambrinos 2000) and ecosystem processes (Crooks 2002; Gordon 1998; Mack et al. 2001). For these reasons land managers often wish to reduce invasive plant populations.

Constraints on management techniques may differ by site or available resources. In some sites, application of some types of herbicides may not be permitted due to presence of features such as open water or designation as environmentally sensitive areas. For example, there is no grass-specific herbicide currently labeled for use in wetland environments (Minnesota Board of Soil and Water Resources 2010). Constraints of cost or labor availability also influence which control methods are available to land managers (Oneto et al. 2010). It is also the case that the nature of the site and its perceived ecological value could influence decisions about whether or not to implement suppression measures at all.

Invasive plant management must be considered in the context of the environment and the surrounding plant community. Population parameters such as fecundity and survivorship can vary between environments; this can result in differing invasive population responses in different environmental contexts (Shea et al. 2005). Furthermore, the efficacy of suppression methods can be context specific (Conn and Seefeldt 2009; Diez et al. 2009), and the response of the non-target plant community may be dependent on initial floristic composition (Barto and Cipollini 2009; Mason and French 2007).

Microstegium vimineum (Trin.) A. Camus (Japanese stiltgrass) is an annual grass invasive throughout the eastern United States. It is tolerant of a wide range of light, moisture, and soil conditions (Claridge and Franklin 2002; Cole and Weltzin 2004). These wide environmental tolerances allow it to invade a variety of habitats which occur throughout much of the eastern deciduous forest: streambanks, floodplains, wetlands, along roads and trails, and in forests following logging and

other forms of disturbance (Cole and Weltzin 2004; Marshall and Buckley 2008; Redman 1995). However, environmental conditions can influence its population growth (Nord et al. 2010; Rauschert et al. 2010).

The sensitivity of *M. vimineum* to a variety of herbicides has been well established (Judge et al. 2005; Peskin et al. 2005). Judge et al. (2008) evaluated effects of herbicide and mechanical suppression on residual plant communities in pine and mixed pine-hardwood forests in North Carolina, and Flory and Clay (2009) conducted a similar study in southern Indiana mixed hardwood forests. However, no such studies have assessed the importance of site context on management of this important invasive.

The objectives of this study were to compare the efficacy of mechanical and herbicide *M. vimineum* suppression methods in logged forest, wetland, and forest road environments in central Pennsylvania, and to quantify the impacts of these methods on the resident plant community. I chose to evaluate the herbicide treatments with the least possible non-target impacts, the “best option” management choice. In the roadside and upland logged sites sethoxydim, a grass-specific herbicide with no residual activity was used. However, neither sethoxydim nor any other grass-specific herbicide is labeled for use in wetlands. I chose an aquatic formulation of glyphosate, a broad-spectrum herbicide with no residual activity, as the compound permitted in wetland environments that seemed likely to have the fewest non-target effects. I hypothesized that herbicidal treatments would cause greater reductions in the *M. vimineum* populations than mechanical suppression because both sethoxydim and glyphosate are systemic herbicides that kill the entire plant, effectively preventing seed production. However, *M. vimineum* can produce tillers and seed heads from even its lowest leaf axils, so the mechanical method would have to remove every plant below the lowest leaf axils to prevent seed production. I further hypothesized that the “best option” broad-spectrum herbicide in the wetland environment would have a much more detrimental impact on the non-target plant communities than the “best option” selective herbicide in the upland environments, as measured by plant species richness and non-*M. vimineum* cover.

Methods and Materials

Study Site

The study was conducted in the Rothrock State Forest in Centre County, Pennsylvania. The forest lies in the ridge and valley physiographic province, and is dominated by oaks (*Quercus* spp.), red maple (*Acer rubrum*), and hickories (*Carya* spp.). The understory is primarily ericaceous shrubs such as blueberries (*Vaccinium* spp.) and mountain laurel (*Kalmia latifolia*). Soils are of the Hazleton-Laidig-Andover association, derived from sandstone parent material and are acidic (Braker 1981).

Sites were located within an area approximately 9.3 km x 5.8 km. The sites in logged environments were located in the most heavily infested areas of forest stands that had been logged within the previous 5-7 years. These areas were largely heavily-impacted zones such as log landings, the staging areas to which cut logs are hauled and loaded into trucks for removal. The roadside environment was immediately adjacent to limestone-graveled forest roads which were graded annually in the spring; roadside vegetation was mown annually in late summer. Wetland sites were adjacent to either streams or seeps, and dominated by typical wetland plants such as sedges and rushes (*Carex* spp. and *Scirpus* spp.)

Experimental Design and *M. vimineum* Data Collection

In early 2007, four site replicates were selected in each of the three environments. At each disturbed forest and wetland site, three 3 x 3 m plots were established. Plots were 3 x 2 m at the roadside sites in order to stay within the treeless road shoulder vegetation. Pre-treatment *M. vimineum* densities were sampled in June with six 20 x 20 cm frames. In order to assess both within and across-year effects of the suppression treatments, the study was replicated in time (initiated in 2007 and in 2008) to account for interannual variation in plant populations and suppression treatments.

In July 2007, one plot at each site was randomly assigned to receive either mowing or herbicide treatment to kill *M. vimineum*, or no treatment. Both treatments were carried out in July. In all suppression plots, treatment was also applied to 1-m

buffer strip around the plot to minimize seed input from plants outside the plot. Mechanical treatment was accomplished with a gasoline-powered string trimmer. The herbicide treatment in the disturbed forest and roadside plots consisted of sethoxydim (Poast) at 30.6 ml active ingredient in 7.5 liters of water with 75 ml concentrated crop oil, broadcast over the plots with a hand-operated 2-gallon handheld sprayer. The aquatic formulation of glyphosate (Rodeo) was applied to the wetland sites at the rate of 206.6 ml active ingredient in 7.5 liters of water with 75 ml concentrated crop oil. This is equivalent to 0.49 kg active ingredient sethoxydim per ha (0.44 lb/acre) and 8.02 kg acid equivalent glyphosate per ha (7.16 lb/acre).

In late September and early October, seed production was estimated in the plots as follows. I determined the relationship between plant size and seed production by measuring the height of 50 unbranched *M. vimineum* plants and 75 *M. vimineum* tillers and counting seeds produced in each plant and tiller. Linear regression was used to establish a relationship between plant length and number of seeds, with separate regressions for unbranched stems and for tillers. Preliminary analysis indicated that the relationship was not different between environment types, so measurements from all environments were pooled in the regressions. In the treated plots, survivors in the entire plot or a representative one-half or one-fourth were measured *in situ*, and the plant height-seed relationship was used to estimate number of seeds produced. Seed production in the untreated control plots was estimated by measuring at least 50 plants in each plot.

In June 2008 *M. vimineum* densities were sampled with twelve randomly-located 20 x 20 cm frames in all plots established the previous year; more frames were used for sampling as there was now greater variability in density throughout the plots.

For the 2008 start of the experiment two 1.5 m x 1.5 m plots were established at each site and randomly assigned to mowing or herbicide treatment. New plots were sufficiently near previously established untreated control plots that no new control plots were established. Prior to treatment, *M. vimineum* densities were sampled as in 2007. In late July herbicide and mowing treatments were applied to all plots with the same methodology as in 2007.

In late September and early October seed production was again estimated in all the plots. To accomplish this, 34 more *M. vimineum* plants and tillers were measured and seeds counted to establish the regression, and surviving *M. vimineum* plants in the plots were measured as before.

In 2009 density was sampled as before, with eight 20 x 20 cm frames to sample density in the smaller 2007-entry plots. Herbicide treatments were applied as in previous years, but mowing was done in late August, not July. Seed production in the plots was again estimated by measuring the stem length and seed production of 61 surviving unbranched plants and 38 tillers to establish the relationships. *M. vimineum* densities in all plots were sampled again in June 2010.

Seed production was estimated as follows. For each year, for unbranched stems and tillers separately, number of seeds per stem or tiller was regressed against stem or tiller length. All data were log-transformed to reduce heteroscedasticity. These relationships, with the measurements of surviving plants, were used to calculate seed production in the plots.

All analysis was performed using R statistical computing software, version 2.9.2 (The R Development Core Team 2009). The R package “nlme” (Pinheiro et al. 2010) was used to perform linear mixed effects analyses of *M. vimineum* density, percent of plot area not covered by vascular plants, and plant species richness. The repeated measures nature of these models was addressed by including treatment year as a fixed factor and plot as a random factor. Tukey’s test was performed in R with the “multcomp” package (Hothorn et al 2008). All tests used a significance level of $\alpha = 0.05$.

Plant Community Composition and Floristic Quality Assessment

In July 2007, all species present in the plots were identified prior to application of treatments. This data collection was repeated every July; therefore, data collected in 2008 reflects response to one year of treatment application. In the 2008-entry plots, percent cover of all plant species present in the central 1 x 1 m was visually estimated using a 1 x 1 m frame divided into 25-cell grid; this was done in July prior to first treatments and every following July.

Floristic quality assessment (FQA) is a method for evaluating the composition of plant communities first proposed by Swink and Wilhelm (1994), based on a coefficient of conservatism (C) between 0 and 10 which is assigned to each species in a given physiographic region. Non-native species have a C of 0. Habitat generalists and plants highly tolerant of disturbance are assigned low coefficient values, and species that are intolerant of disturbance and display a high degree of habitat specificity are assigned higher coefficients. Therefore, a plant community with a low FQA index is indicative of a more degraded environment than one with a high FQA index. I used an index developed for the mid-Atlantic region (Chamberlain and Ingram in preparation), using the values listed for the ridge and valley ecoregion, to assign C values to each species identified in the plots (Table A3). Where identification was possible only to the genus level due to lack of reproductive structures, I used the value of the lowest-rated species in that genus. I summed the C values for each plot both pre-treatment (2007 and 2008) and in 2010, divided this total by the number of species in the plot to derive a quality score I (Miller and Wardrop 2006), and used the difference in the I scores between 2007 and 2010 as an indicator of changes in floristic quality in the plots.

For multivariate analysis of plant community data, a matrix was constructed for each entry year with a column for each species and a row for each plot in both start and end years. In the 2007-entry matrix elements were 1 and 0 for presence/absence, and in the 2008 matrix elements were percent cover estimates for each species. As these algorithms analyze patterns of redundancy in the data, all species appearing in less than three plots were removed from the data sets (McCune and Grace 2002), and the data were normalized by column maxima. The Sorensen distance measure was used in calculating all distance matrices. NMS ordination of plant community data was performed with PC-ORD. The “adonis” function in the “vegan” package of R was used for multivariate analysis of variance. This was done separately for plots initiated in 2007 and 2008, with the normalized distance matrix as the response and treatment, environment type, and year (two levels, pre-treatment and final) as factors.

To analyze responses of broader vegetation categories, percent cover in the 2008 plots started in 2008 was summed into the following functional categories: herbaceous dicot, woody dicot, fern, and non-*M. vimineum* graminoid (including grasses, sedges, and rushes) for beginning and ending years. Linear mixed-effects models were used to evaluate responses of percent cover in each category to treatment, environment, and year (beginning and end).

Results

M. vimineum population density

M. vimineum densities in all treatment plots decreased dramatically as soon as suppression began (Figure 3.1). Initial mean densities were between 4200 and 5600 stems m⁻², with the lowest densities in the roadside plots. After one year of suppression, re-emergence in treatment plots sampled the following June fell to less than 700 stems m⁻². After three years of suppression, densities sampled the following June were less than 100 stems m⁻². Densities after 2 years of treatment tended to be lower in herbicide plots than in mown plots in all environments for plots of both entry years, but the difference was significant only in the logged 2007-entry plots (Figure 3.2). After three treatment years in 2007-entry plots, *M. vimineum* densities were not significantly different between treatments. In logged and roadside environments, densities tended to be lower in herbicide than in mown plots, but in the wetland environment they were higher (Figure 3.2). In three of the four 2007-entry wetland sites, final *M. vimineum* densities were at or near 0, but in the fourth site the average density in the herbicide plot had increased from an average of 9 stems m⁻² in 2009 to 535 stems m⁻² in 2010. Mean *M. vimineum* densities in the unmanaged plots in 2008 and 2009 did not differ significantly from initial densities. The lowest untreated control plot densities, 2167 stems m⁻² ± 652 (mean ± SE), were recorded in 2010, a dry year in which April-June rainfall totaled only 68% of the 30-year average.

Median stem counts tended to be lower in herbicide plots than in mown plots in all environments in all years following the first treatment (Table 3.1). Median stem counts in herbicide plots were 0 in all three environments by the third treatment year.

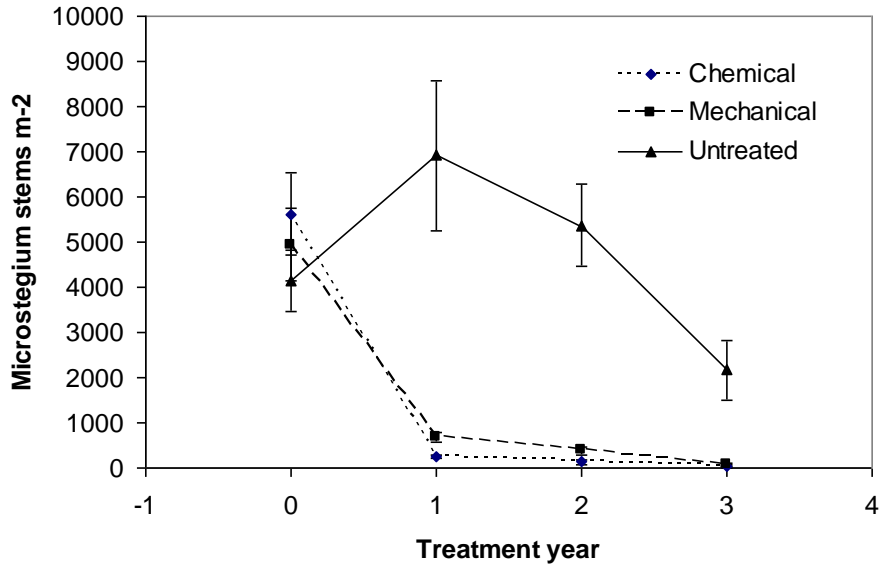


Figure 3.1. *M. vimineum* densities (mean \pm SE) in chemically suppressed, mechanically suppressed, and untreated control plots throughout the experiment.

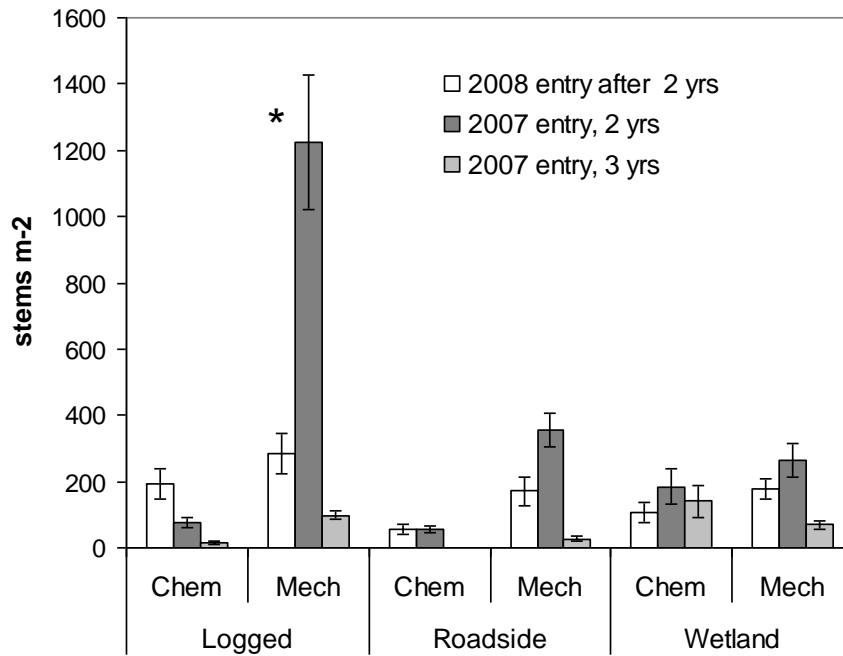


Figure 3.2. *M. vimineum* densities (mean \pm SE) in chemically and mechanically suppressed plots in three environments after two treatment years for both entry years, and after three treatment years for 2007 entry plots. The only mean significantly different from the others is marked with a star. Recall that initial *M. vimineum* densities exceeded 4000 stems m⁻².

Environment	Treatment	Treatment year			
		0	1	2	3
Logged	Chemical	4312.5	162.5	50	0
	Mechanical	4387.5	600	375	75
Roadside	Chemical	2137.5	75	25	0
	Mechanical	2075	375	162.5	25
Wetland	Chemical	4237.5	125	25	0
	Mechanical	3775	350	125	50

Table 3.1. Medians of density counts from 20 x 20 cm frames, scaled up to reflect stems m⁻², by treatment types and environments.

Seed production

The relationships between the length of single stems or tillers and number of seeds produced on those stems and tillers were reasonably strong, with adj. R-sq ranging from 72.2 to 93.2 (Table A1).

Mean seed production in untreated control plots was higher in wetland and logged plots than in roadside plots. For example, in 2007 mean seed production in the untreated control plots was estimated at 400,480 seeds m⁻² in wetland and 366,957 seeds m⁻² in logged environments, but only 114,740 seeds m⁻² in the roadside. Seed production in the mown plots showed a great deal of variability in 2007 and 2008, with no consistent trends (Figure 3.3). Despite the magnitude of the variability, the estimated seed production in the mechanically-treated plots was always less than 1% of estimated production in the untreated control plots. Seed production in these plots was much lower in 2009, averaging less than 110 seeds m⁻² in all three environments.

No seeds were produced in any herbicide plot in any year, with the exception of one roadside plot in which fewer than 10 seeds were produced in the first year.

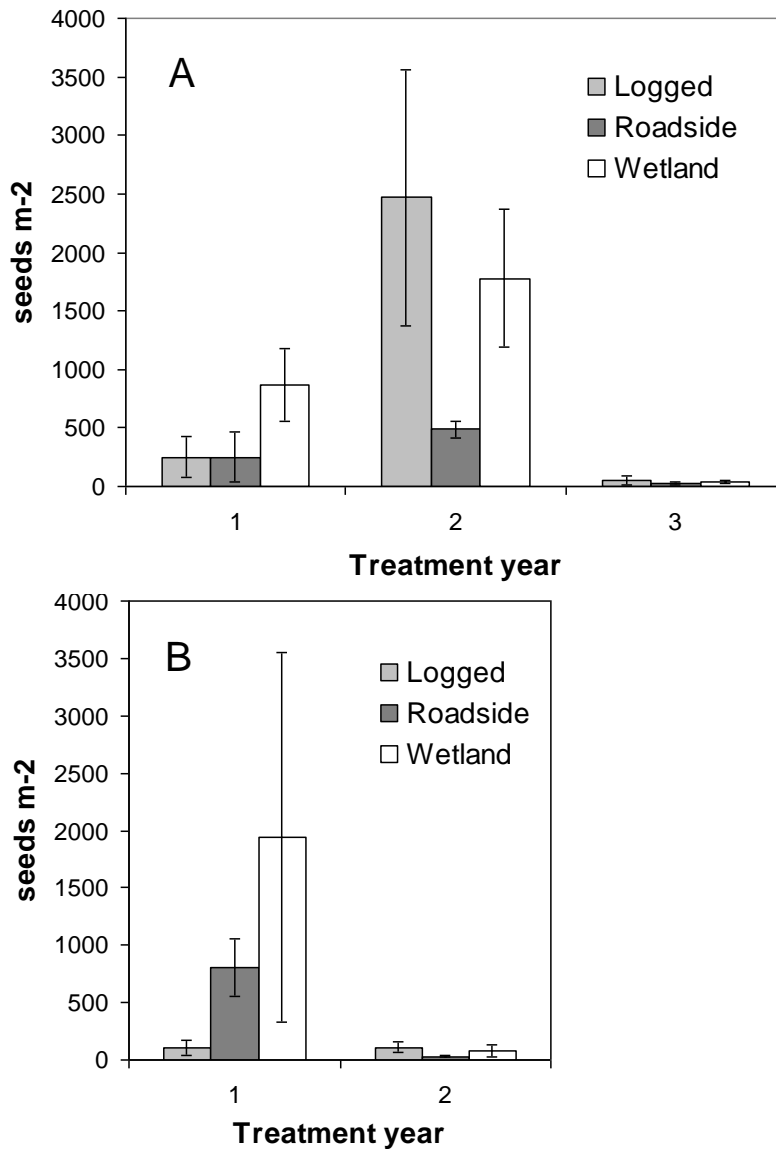


Figure 3.3. Estimates of *M. vimineum* seed production in mechanical treatment plots (mean \pm SE) in three environments throughout the course of the experiment, for A) 2007 entry plots and B) 2008 entry plots.

Unvegetated Ground

The percent of plot area which was bare (not covered by vascular plants) at the time of the July surveys increased markedly in almost all treatment plots over the course of the experiment, signaling an overall reduction in the plant communities. Initially, bare ground accounted for between four and 14 percent of the plot area. At the end of the experiment, mean unvegetated area in the treatment plots exceeded

35% in all treatment-environment combinations except mechanically treated plots in the wetland environment. Unvegetated ground increased slightly in the unmanaged plots as well due to drought conditions in 2010, to a mean of about 18%.

Pairwise comparisons with Tukey’s test reveal that all treatment plots in all environments ended with significantly more unvegetated area than untreated control plots, except for mown plots in the wetland environment (data not shown). In the 2007 entry plots the final bare ground estimate did not differ between herbicide and mechanical plots in any environment. However, in the 2008 entry the chemical plots had significantly more unvegetated area than did the mown plots (Figure 3.4).

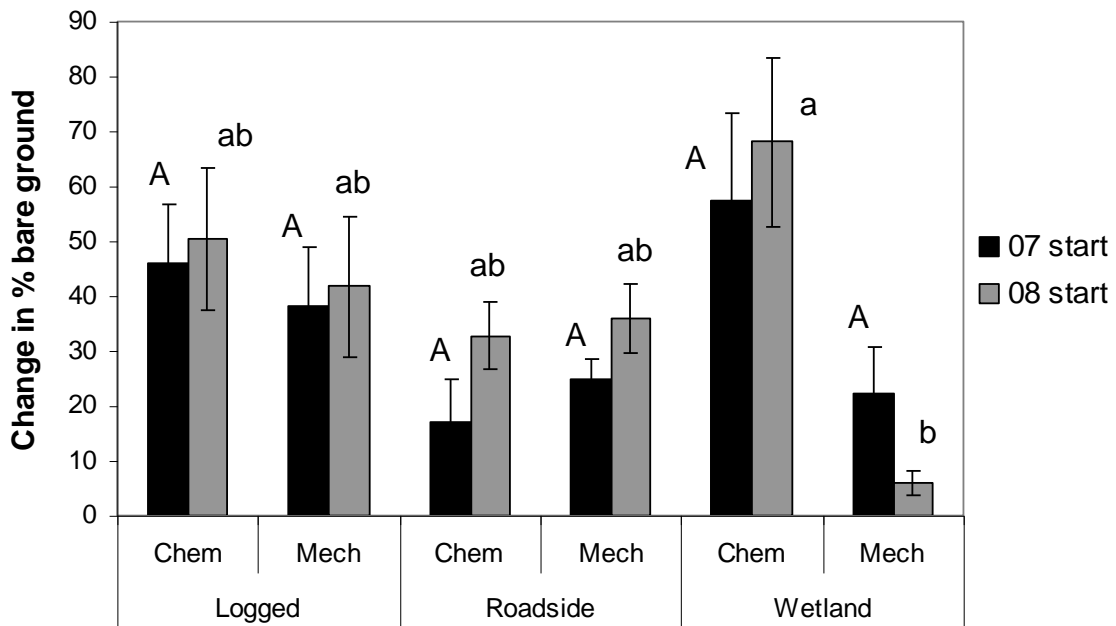


Figure 3.4. Increase in percent of plots consisting of bare (unvegetated) ground in treatment plots in three environments (mean \pm SE), calculated by subtracting the pre-treatment estimate from the 2010 estimate. Thus, for 2007 entry plots, this reflects three years of treatment application (Tukey’s multiple comparisons in uppercase); for 2008 entry plots this reflects two years of treatment (Tukey’s multiple comparisons in lowercase).

Species Richness

At the initiation of the study and prior to implementing any of the suppression treatments, species richness did not differ by assigned treatment group. Environment

type was significant, however, with the highest number of species present in roadside and lowest in logged plots in both entry years. Initial species richness in the 2007 entry plots (mean 13.8) was higher than that of the smaller 2008 plots (mean 7.2).

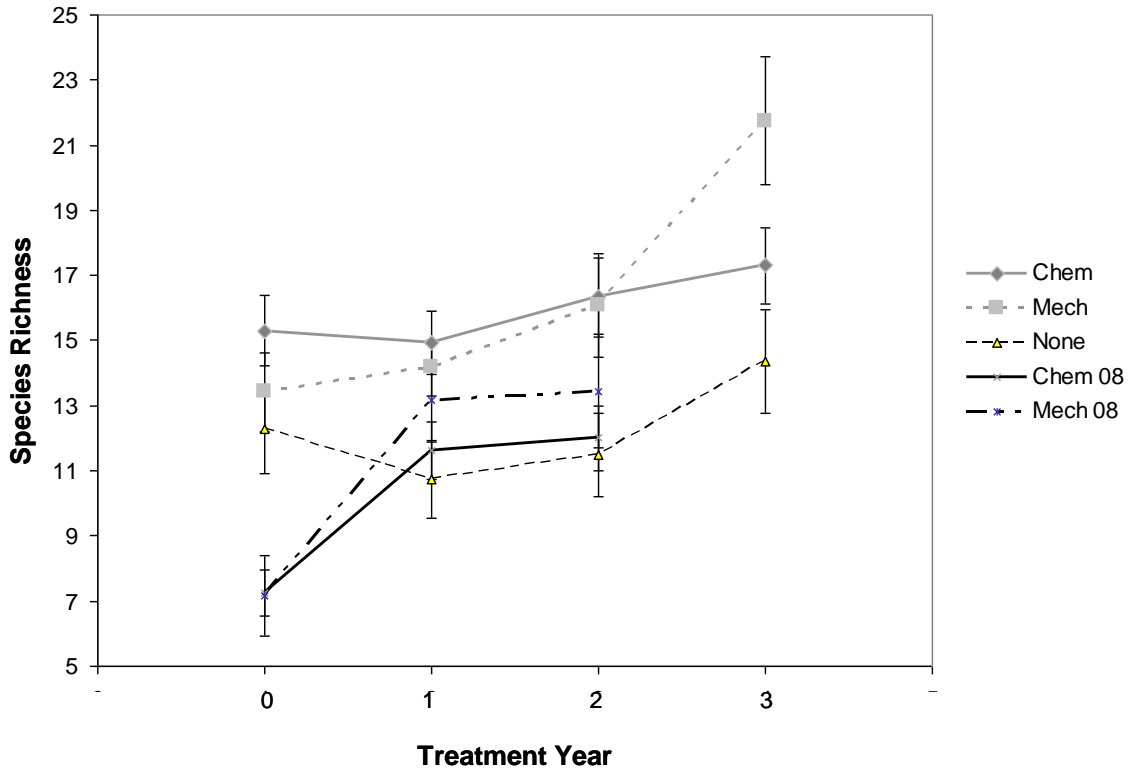


Figure 3.5. Number of vascular plant species present in the plots throughout the experiment, in three treatment groups (mean \pm SE). Values in year 0 indicate pre-treatment conditions. Note that there are three post-treatment years of data for 2007-entry plots and two post-treatment years for 2008-entry plots.

Species richness increased in 41 of the 48 plots in which *M. vimineum* was suppressed (Figure 3.5). The increase was particularly noticeable in the 2008 entry plots which due to their smaller size had lower species richness initially. After only one year of *M. vimineum* suppression species richness increased by 40 to 80 percent. After two years of *M. vimineum* suppression treatments, plant species richness in the plots was not significantly different between suppression treatments (Table 3.2). However, after three treatment years in the 2007-entry plots there were marginally

significant differences by treatment type, with highest mean species richness (21.8 species per plot) in the mechanically-treated plots (Figure 3.6). Change in *M. vimineum* cover in 2008-entry plots was not a significant predictor of change in species richness.

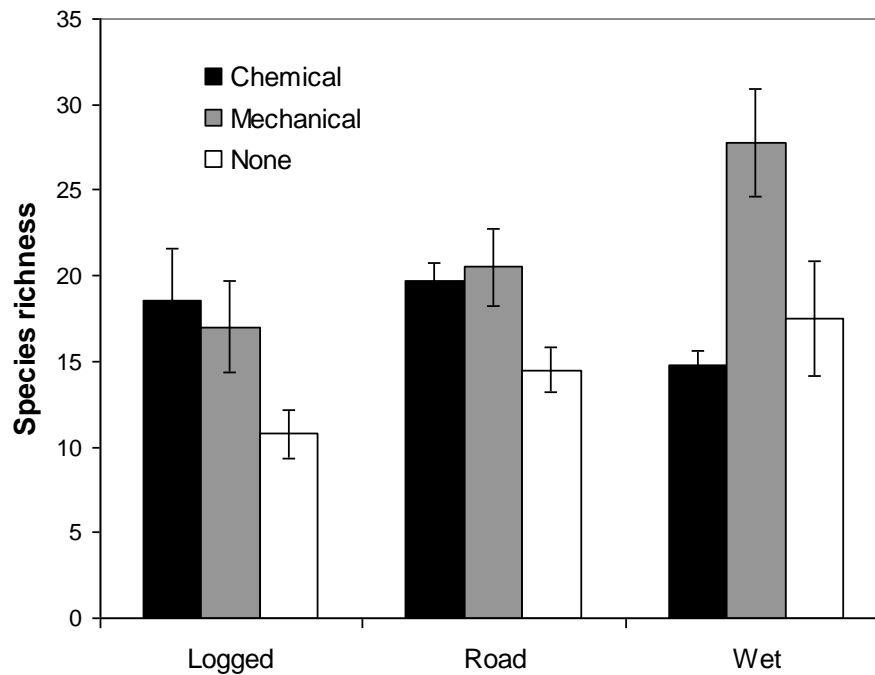


Figure 3.6. Plant species richness in 2007 entry plots (mean \pm SE) measured after 3 treatment years, in three treatments in three environments.

		numDF	denDF	F-value	p-value
2008 entry plots	trt	1	16	1.509426	0.237
	env	2	16	3.365006	0.0603
	trt * env	2	16	2.376716	0.1248
	pre-trt spp	1	16	0.048751	0.828
2007 entry plots	trt	2	26	2.656946	0.0891
	env	2	26	1.807409	0.1841
	trt * env	4	26	4.420055	0.0074
	pre-trt spp	1	26	9.890066	0.0041

Table 3.2. Analysis of variance for linear mixed models of species richness in plots of both start years, with plot as random.

Plant Community Composition

Pre-treatment plant communities were evaluated for similarity of species composition between treatment groups and environment types using multivariate analysis of variance. This was done with presence/absence data for 2007 entry plots and with percent cover data for 2008 entry plots. Composition differed between all environment types ($F=13.88$, $p=0.0002$), but not between assigned treatment groups ($F=0.4011$, $p=0.9630$). Plant community composition in the plots in 2010 differed significantly from pre-treatment composition (year effect was significant), but types of treatment did not differ from each other (Table 3.3). No interaction terms were significant so they were removed from the models.

NMS ordination and cluster analysis also failed to reveal similarities in final plant species composition within treatment groups in plots of either entry year.

In the analyses performed on vegetation groups (herbaceous dicots, woody dicots, ferns, and non-*M. vimineum* graminoids), treatment was not a significant factor in any model (Table 3.4). Environment was significant in the non-*M. vimineum* graminoids model, with higher non-*M. vimineum* graminoid cover in wetland plots. The year of the experiment was highly significant in the dicots model, with greater dicot cover at the end of the experiment than at beginning.

		Df	SumsOfSqs	MeanSqs	F.Model	Pr(>F)
2007 plots	env	2	5.66541	2.8327	18.00245	0.001996 **
	Trt	2	0.43438	0.21719	1.38028	0.143713
	Year	1	0.59707	0.59707	3.79451	0.001996 **
	Residuals	66	10.38517	0.15735		
	Total	71	17.08203			
2008 plots	env	2	1.83872	0.91936	3.97069	0.001996 **
	trt	1	0.29052	0.29052	1.25473	0.223553
	year	1	3.4588	3.4588	14.93845	0.001996 **
	Residuals	43	9.95607	0.23154		
	Total	47	15.5441			

Table 3.3. Multivariate analysis of variance evaluating differences in plant species composition in the plots. For 2007 plots the response matrix consist of species presence/absence data at the beginning of the experiment and following three years of treatment application. For analysis of 2008 plots the response matrix consists of

percent covers of plant species present pre-treatment and after 2 years of treatment application.

		numDF	denDF	F-value	p-value
Non-stiltgrass graminoids	Trt	1	19	0.484662	0.4947
	Env	1	19	0.548266	0.4681
	Year	1	23	3.399642	0.0781
	Trt * Env	1	19	2.122497	0.1615
Woody dicots	Trt	1	19	2.803219	0.1105
	Env	1	19	2.64176	0.1206
	Year	1	23	1.169854	0.2906
	Trt * Env	1	19	1.434818	0.2457
Herbaceous dicots	Trt	1	19	0.81085	0.3791
	Env	1	19	1.2065	0.2858
	Year	1	23	38.13522	<.0001
	Trt * Env	1	19	2.25423	0.1497
Ferns	Trt	1	19	0.109851	0.7439
	Env	1	19	0.093404	0.7632
	Year	1	23	1.990658	0.1717
	Trt * Env	1	19	0.053747	0.8191

Table 3.4. Linear mixed effects models for vegetation groups. Factors were treatment type, environment type, and treatment year (levels of pre-treatment and final year); plot was a random effect.

Four other invasive species were found in the 2008-entry plots. Canada thistle (*Cirsium arvense*) decreased in both of the plots in which it was present prior to treatment, while in another plot it was not present initially but at the end of the experiment occupied 3% of the plot. Crown vetch (*Coronilla varia*) initially covered 1% of one roadside plot; after two treatment years it had increased to 3%. Japanese barberry (*Berberis thunbergii*) increased from 0.5 % cover to 1% and 2% in the two roadside plots where it occurred. Hay-scented fern (*Dennstaedtia punctiloba*), a native species which acts as an invasive in northeastern forests (de la Cretaz 1999), occurred only in the logged environment. It disappeared from one plot where it initially represented 2% of the plant cover, but in two other plots where it was not initially present it eventually covered 10% and 20%.

Floristic quality changes tended to be most negative in the chemically suppressed wetland plots (Figure 3.7). Due to the high degree of variability, however, differences were not significant and no treatment effect was significantly different from zero.

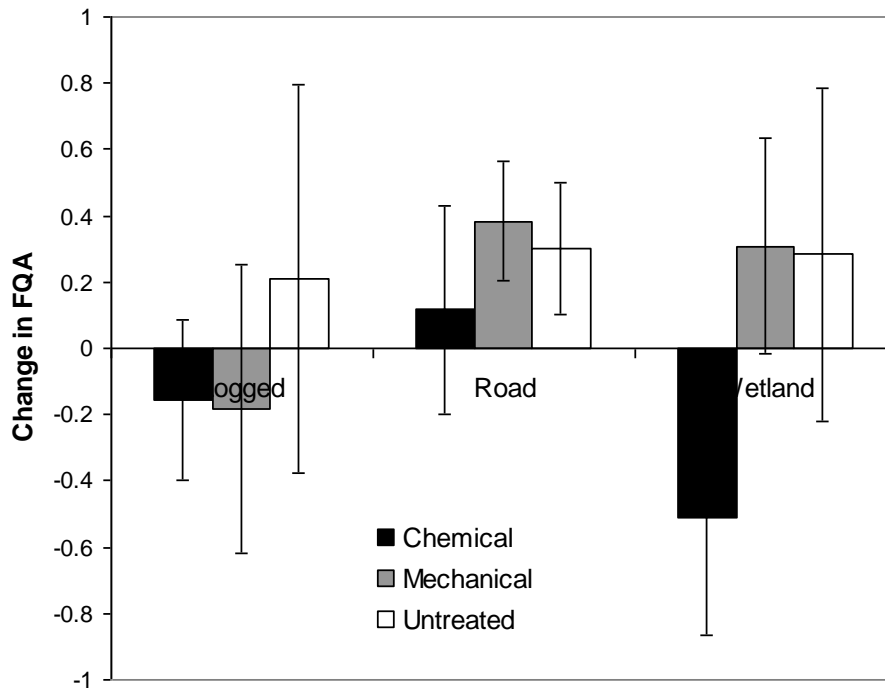


Figure 3.7. Change in floristic quality assessment values in 2007 entry plots, in three treatments in three environments. This is shown as the 2007 assessment values subtracted from the 2010 assessment values.

Discussion

Both herbicide and mowing treatments resulted in very significant reductions in *M. vimineum* populations in all environments in all years. This is consistent with other studies which have demonstrated that many methods of suppression can reduce *M. vimineum* populations, including various herbicide regimes (Judge et al 2005) as well as non-chemical techniques (Flory and Lewis 2009). The median density of *M. vimineum* was lower in the herbicide treated than mown plots in every environment in

every year, and in the final year of the experiment were zero in all the herbicide treatment plots. This suggests that the herbicide treatments tended to have a greater impact on *M. vimineum* populations. However, the lack of statistically significant differences between the means highlights the variability of the results. Judge et al (2008) also found no significant differences in *M. vimineum* cover reduction between hand weeding, string trimming, and grass-specific herbicide (fenoxaprop-P) treatments.

I attribute the reduction in *M. vimineum* densities in untreated control plots in 2010 to the drought conditions at the beginning of that growing season. That year, total precipitation for April, May and June totaled 184 mm, while the 30-year average total for those months is 272 mm (Penn. State Univ. Dept. of Meteorology 2011). *M. vimineum* populations can be reduced by drought (Webster 2008, Gibson 2002). It is also likely that the reduction of vegetative cover in the untreated control plots was due to the drought as well.

Seed production was almost completely suppressed with glyphosate and sethoxydim; the only seeds set in herbicide treated plots throughout the course of the experiment were a few seeds in the roadside environment in 2007. That year, weather preceding herbicide application was very dry. Therefore it is likely that herbicide uptake was reduced, so a few plants survived the treatment. No *M. vimineum* survived the herbicide treatments in the logged forest and wetland environments, where moisture stress was less severe. Peskin et al. (2005) also found complete suppression of seed production with sethoxydim, and 99% suppression with glyphosate.

Despite the fact that almost no seeds were produced in the herbicide treatment plots, but were produced sometimes by the thousands in every mown plot in every year, I saw no statistically significant differences between treatments in the June density seedling counts. This again underlines the variability of these results, as well as the importance of the soil seed bank in short-term population persistence. The soil seed bank seems less important in central Pennsylvania populations than further south, however; Judge et al. (2008) saw *M. vimineum* cover increase by 10% relative

to unmanaged plots in the first year following mechanical and herbicide treatment, which they attributed to the soil seed bank.

The differences in *M. vimineum* density and seed production in mechanical treatment plots between 2009 and 2010 illustrate the importance of timing mechanical treatments, as well as site-specific challenges in achieving adequate control with mechanical methods. Treatment in 2008 was applied in late July. The quantity of large branches on the ground in some of the mechanical treatment plots made it impossible to mow the *M. vimineum* low enough to kill it all. By late September, many stems had resumed growth at surviving lower nodes and were large enough to produce many seeds. This is reflected in the 2009 density counts. In contrast, in 2009 treatment was applied in late August, so the surviving nodes had very little time to regrow. Seed production and the following summer seedling density counts were low. *M. vimineum* was more easily suppressed with the string trimmer in the roadside and some wetland plots where the ground surface was much less uneven.

M. vimineum population densities in herbicide treatments tended to be lower at the end of the experiment than densities in mown plots, with the exception of one outlier wetland site. The wetland site in which the herbicide plot ended with a high *M. vimineum* density was situated in a low area surrounding a stream, which flooded sometime between fall 2009 and spring 2010. By the time of the July 2010 population sampling, approximately two-thirds of the plot nearest the stream was covered by *M. vimineum*, most likely from seeds delivered from upstream populations by the flood. The remainder of the plot remained mostly bare ground.

The analysis of bare ground in the treatment plots helps explain the fate of this plot. The herbicide used in wetland plots was glyphosate. Although labeled for use in wetlands, this broad-spectrum herbicide eliminated not only the *M. vimineum* but most of the other vegetation as well, leaving an average of 70% of the ground unvegetated. This made these plots extremely vulnerable to reinvasion when *M. vimineum* propagules were delivered by the flooding event, as predicted by the fluctuating resource availability theory of invasion (Davis et al 2000). The increase in bare ground also enables the establishment of other invasive species, as illustrated by the invasion of two plots by hay-scented fern and the increases in cover of crown

vetch, dandelion, and Japanese barberry. These increases were small, however, compared to the 23% increase in exotic cover reported by Judge et al (2008) in mechanically-treated plots in southern forests.

I found significant differences in the final amount of unvegetated ground between the unmanaged and the treated plots. More evidence for the variability of control outcomes across environmental conditions is found in a comparison of these results with those of Flory (2009), who in southern Indiana forests found no difference in the amount of bare ground between plots which had received no treatment, hand weeding, and grass-specific herbicide.

Species richness increased in almost all of the plots in which *M. vimineum* was suppressed, but treatment differences in species richness were not seen until the third year of treatments when greater increases were observed in mown plots than in herbicide plots. Longer-term studies with larger plots would be needed to resolve the question of whether herbicide and mechanical methods of *M. vimineum* suppression ultimately drive plant community composition in different directions. The only clear trend I observed was an increase in dicot cover with both treatment types, consistent with similar observations by Flory and Clay (2009). Flory and Clay (2009) also observed significant decreases in graminoid cover in plots treated with the grass-specific herbicide fluazifop-P-butyl. My grass-specific herbicide treatment did not result in significant reductions in graminoid cover, possibly because sethoxydim appeared to have little effect on the perennial grasses such as *Leersia virginiana* commonly found in my study sites.

The patterns in floristic quality changes also highlight the differences in impact on non-target plant community between “best-option” herbicides in the different environments. In the logged plots with the selective herbicide, there tended to be little difference in the increase in floristic quality between mown and herbicide plots. However, in the wetland environment where the broad-spectrum herbicide was used, the herbicide plots showed a marked decrease in floristic quality. This is to be expected as the herbicide affected all plants in the plots, not just the *M. vimineum*.

That multivariate analysis of plant community composition did not reveal any patterns may mean that my plot size or replication was too small to resolve this

question, or it may simply reflect an inherent lack of predictable pattern in plant community changes following suppression of *M. vimineum*.

My results suggest that the “best” suppression technique may vary with site conditions, and that there may be tradeoffs between *M. vimineum* suppression and release of more desirable species. This study suggests that on roadside and logged forest sites, a grass-specific herbicide is the best technique as it is quickly and easily applied and its efficacy is less affected by unevenness of the ground and downed wood left by the logging process. Damage to the residual plant community is no greater than that from mechanical treatment as judged by amount of ground left bare and the changes in floristic quality. However, even in these environments species richness gains in herbicide plots were not as great as in mown plots. In wetland sites, however, where the choice of chemicals is limited, mechanical treatment is preferable: while its effect on *M. vimineum* populations may be slightly less suppressive, its effect on the residual plant community is less detrimental than that of the best available herbicides.

In conclusion, my results highlight the need to think about efficacy of invasive plant control in a broader sense than simply reduction of invasive populations. A definition of control efficacy must also address the invasibility of the community left after treatment. The “best” suppression techniques may not be the one which simply results in greatest reduction of the invasive populations or suppression of seed production; it may be the one which provides the best combination of suppressing invasives while leaving the surrounding plant community as intact as possible. It is not difficult to kill *M. vimineum* and prevent seed production; however, if this occurs at the expense of native plant cover and leaves the area open to reinfestation, the value of this temporary suppression is doubtful. Thus the key challenge in *M. vimineum* management is not population reduction, which is relatively easily to achieve; rather it lies in preventing propagule spread and re-invasion of treated areas, and in re-establishment of native plant communities.

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Literature Cited

- Baiser B, Lockwood JL, La Puma D and Aronson MFJ (2008) A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. *Biological Invasions* 10: 785-795
- Barto EK and Cipollini D (2009) Garlic mustard (*Alliaria petiolata*) removal method affects native establishment. *Invasive Plant Science and Management* 3: 230-236
- Braker WL (1981) Soil Survey of Centre County, Pennsylvania. USDA-SCS, Washington, D.C.
- Chamberlain SJ and Ingram HM (in preparation) Developing coefficients of conservatism to advance floristic quality assessment in the Mid-Atlantic region.
- Claridge K and Franklin SB (2002) Compensation and plasticity in an invasive plant species. *Biological Invasions* 4 339-347
- Cole PG and Weltzin JF (2004) Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeastern Naturalist* 3: 545-562
- Conn JS and Seefeldt SS (2009) Invasive white sweetclover (*Melilotus officinalis*) control with herbicides, cutting, and flaming. *Invasive Plant Science and Management* 2: 270-277
- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97: 153–166
- Diez JM, Buckley HL, Case BS, Harsch MA, Sciligo AR, Wangen SR and Duncan RP (2009) Interacting effects of management and environmental variability at multiple scales on invasive species distributions. *Journal of Applied Ecology* 46: 1210-1218
- Flory SL (2009) Management of *Microstegium vimineum* invasions and recovery of resident plant communities. *Restoration Ecology* 18: 103-112
- Flory SL and Clay K (2009) Invasive plant removal method determines native plant community responses. *Journal of Applied Ecology* 46: 434-442

- Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. *Ecological Applications* 8: 975-989
- Hejda M, Pysek P and Jarosik V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97: 393-403
- Hothorn, T., F. Bretz, and P. Westfall. 2008. multcomp: Simultaneous Inference in General Parametric Models. R package version 1.2-4.
- Judge CA, Neal JC and Derr JE (2005) Preemergence and postemergence control of Japanese stiltgrass (*Microstegium vimineum*). *Weed Technology* 19: 183-189
- Judge CA, Neal JC and Shear TH (2008) Japanese Stiltgrass (*Microstegium vimineum*) Management for Restoration of Native Plant Communities. *Invasive Plant Science and Management* 1: 111-119
- Lambrinos JG (2000) The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered mediterranean-type shrubland in California. *Diversity and Distributions* 6: 217-231
- Mack MC, D'Antonio CM and Ley RE (2001) Alteration of ecosystem nitrogen dynamics by exotic plants: A case study of C-4 grasses in Hawaii. *Ecological Applications* 11: 1323-1335
- Marshall JM and Buckley DS (2008) Effects of microsites created by selective harvesting on growth of *Microstegium vimineum* in a central hardwood forest. *Forest Science* 54: 534-542
- Mason TJ and French K (2007) Management regimes for a plant invader differentially impact resident communities. *Biological Conservation* 136: 246-259
- McCune B and Grace JB (2002) *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR, 300 pp
- McCune, B. and M. J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5. MjM Software, Gleneden Beach, Oregon, U.S.A.
- Miller, S.J. and D.H. Wardrop. 2006. Adapting the floristic quality assessment index to indicate anthropogenic disturbance in central Pennsylvania wetlands. *Ecological Indicators* 6: 313-326
- Minnesota Board of Water and Soil Resources. 2010. Planting and maintenance recommendations for wetland restoration and buffer projects. Accessed 1-7-2011. http://www.bwsr.state.mn.us/native_vegetation/planting-maintenance-recs.pdf
- Nord AN, Mortensen DA and Rauschert ESJ (2010) Environmental factors influence early population growth of Japanese Stiltgrass (*Microstegium vimineum*). *Invasive Plant Science and Management* 3: 17-25
- Oneto SR, Kyser GB and DiTomaso JM (2010) Efficacy of mechanical and herbicide control methods for Scotch broom (*Cytisus scoparius*) and cost analysis of chemical control options. *Invasive Plant Science and Management* 3: 421-428

- Oswalt CM, Oswalt SN and Clatterbuck WK (2007) Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *Forest Ecology and Management* 242: 727-732
- Pennsylvania State University Department of Meteorology 2011. Joel N. Myers Weather Center home page. Accessed 1-9-2011.
<http://bub2.meteo.psu.edu/WXSTN/wxstn.htm>
- Peskin N, Mortensen DA, Jones BP and Booher MR (2005) *Ecological Restoration* 23: 64-65
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and the R Development Core Team. 2010. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-97.
- R Development Core Team 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rauschert ESJ, Mortensen DA, Bjornstad ON, Nord AN and Peskin N (2010) Slow spread of the aggressive invader, *Microstegium vimineum* (Japanese stiltgrass). *Biological Invasions* 12: 563-579
- Redman DE (1995) Distribution and habitat types for Nepal microstegium [*Microstegium vimineum* (Trin.) Camus] in Maryland and the District of Columbia *Castanea* 60: 270-275
- Shea K, Kelly D, Sheppard A and Woodburn T (2005) Context-dependent biological control of an invasive thistle. *Ecology* 86: 3174-3181
- Silveri A, Dunwiddie PW and Michaels HJ (2001) Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. *Biological Invasions* 3 379-389
- Swink F and Wilhelm G (1994) *Plants of the Chicago Region*. Indiana Academy of Science, Indianapolis, IN, 932 pp
- Wearne LJ and Morgan JW (2004) Community-level changes in Australian subalpine vegetation following invasion by the non-native shrub *Cytisus scoparius*. *Journal of Vegetation Science* 15: 595-604

Chapter 4

Fates of *Microstegium vimineum* seeds in the soil

Abstract

Microstegium vimineum (Japanese stiltgrass) is an annual grass which is invasive in a variety of environments. Work with weeds in agricultural systems has shown that seed mortality and persistence in the soil can be influenced by environmental factors. A buried seed bag study was initiated to compare seed fates between *M. vimineum* in wetland, logged forest, and forest roadside environments. Sets of seed bags were buried in each environment in 2007 and in 2008, and retrieved annually in April, June, August, and October through 2010. Germination rates in the first growing season after burial averaged $56.3 \pm 9.3\%$ and $79.3 \pm 7.9\%$ for bags buried in 2007 and 2008, respectively, with first-year germination rates in the roadside at least 15 percentage points higher than in the other environments. Fewer than 4% of the seeds in the study died without germinating. When an exponential decay model was fit to the dormant seed data from all retrieval dates, the decay constant was significantly different between environments, greatest in the roadside and least in the logged environment. That the seed bank is shorter-lived on the roadsides means that *M. vimineum* populations may be more easily suppressed in that environment than in logged or wetland areas.

Introduction

Invasive plants present an increasing challenge to land managers. Understanding seed bank dynamics is crucial to management and particularly to eradication efforts (Panetta 2007). In particular, seed longevity and germination rate are key parameters in determining duration of eradication effort (Cacho et al. 2006). An understanding of seed bank dynamics is also needed to inform population models of problem plants (Van Mourik et al. 2005).

Microstegium vimineum (Japanese stiltgrass) is a grass of Asian origin that is invasive in a variety of environments throughout the eastern United States, including wetlands, floodplains, stream banks, along forest roads, and in forests interiors,

particularly after disturbances such as timber harvest. Its ecological impacts include reducing native plant diversity, impeding forest regeneration, and altering the soil environment (Ehrenfeld et al. 2001; Oswalt et al. 2007, Baiser et al. 2008, Flory 2009, DeMeester and Richter 2010). It grows and reproduces successfully across a wide variety of environmental gradients, including soil types, light, and moisture regimes (Winters et al. 1982, Redman 1985, Claridge and Franklin 2002, Cole and Weltzin 2004). Most germination occurs in late spring and early summer, but can occur throughout the growing season (A. Nord, pers. obs.). **A very high percentage of seeds are viable (Judge2005). (check percentage)** As it is an annual plant, understanding its seed bank dynamics is key to managing its populations (Anderson 2005).

Work with weedy species in agricultural systems has shown that seed bank dynamics can be influenced by environmental factors. Seed longevity can be affected by soil moisture (Schutte et al. 2008), and by soil organic matter which may promote fungal growth (Van Mourik et al. 2005). Germination can be affected by light, oxygen availability, moisture regime, and the chemical environment (Baskin and Baskin 1998). The persistence of dormancy in seeds of grasses has been shown to be influenced by oxygen availability, the chemical environment, and the microbial community (Simpson 1990). The occurrence of *M. vimineum* across such a variety of habitat types raises the question of how differences in environment might influence its seed bank dynamics.

Evidence suggests that *M. vimineum* seed persists at least two years in the soil. Barden (1987) found no seedling emergence in plots where seed production had been prevented for the two previous years. Nord and Mortensen (unpublished data) found some seedling emergence after three years of preventing seed production. Judge (2005) found that seeds are shed with primary innate dormancy that lasted at least 60 days. After 90 and 120 days burial under field conditions, germination in the lab was near 100%, suggesting that few if any seeds remained dormant. However, no research to date has followed the fate of seeds in the soil for more than 120 days.

The objective of this study was to characterize the fates of *M. vimineum* seeds buried in the soil over a period of time spanning three years, quantifying seed loss to

germination and to mortality at regular intervals. I also wanted to compare these fates between three different environments: logged upland forest, wetland, and roadside.

Methods

The study was conducted in Rothrock State Forest, a second-growth oak-hickory forest located in Centre County, Pennsylvania. Large populations of *M. vimineum* have been present in the forest for at least fifteen years. I selected four heavily-invaded sites in each of three environments: logged upland forest, wetland, and along limestone gravel roads.

Mature *M. vimineum* seeds were collected from these sites in October 2007. Seeds from all sites were pooled and stored under refrigeration until burial. Bags of fine nylon mesh (5 cm x 5 cm) were filled with 100 seeds each. In late November and early December 2007 seed bags were buried 30 cm apart, 1 to 1.5 cm below the surface of the soil.

In April, June, August, and October of 2008 one bag was retrieved from each site. Bags were stored under refrigeration until they were processed. In the lab the bags were opened and seeds examined under a dissecting microscope to determine their fates: germinated, decomposed, or still appearing viable. Seeds that had germinated were identifiable by remnants of seedlings adhering to the seed, a split in the seed coat at the point of embryo emergence, and/or a characteristic deflated shape. Decomposed seeds were soft to the touch of the probe, had protrusions caused by fungal growth, and/or were discolored. Seeds that were firm to the touch and not discolored were considered viable.

More seed bags were constructed and buried as described above in November 2008. Thus, at each 2009 sampling data (again, April, June, August, and October) I retrieved one bag of 2007 seeds and one bag of 2008 seeds. In 2010 retrieval occurred in April, June, and October.

In October 2009 I performed tetrazolium staining on all of the seeds which I had classified as dormant and viable after visual assessment, as well as five of the seeds classified as decomposed, in order to confirm the visual assessments. Caryopses

were removed from the hulls, split longitudinally, and incubated for 18 hours at room temperature in a solution of 1% tetrazolium choride. Seeds were then examined with a stereo dissecting microscope to assess viability (Grabe 1970).

I used an exponential decay model $y = e^{-kt}$ to describe the decreasing proportion of seeds remaining viable over time, where y represents viable seed, t represents time since burial of seed bags, and k is the exponential decay constant (Davis et al. 2008; Teo-Sherrell and Mortensen 2000; Washitani 1985). I log-transformed the response variable to fit linear mixed-effects model, using the package nlme (Pinheiro et al. 2009) in the statistical computing software R version 2.13.0 (R Development Core Team 2011). I used plot as a random effect in order to account for the repeated measures nature of the data set. Fixed terms in the model were start year; time since burial; and the interaction of environment type and time since burial, which is the estimate of k for each environment. Environment type itself was not included in the model, as the mean amount of dormant seeds counted in each environment throughout the course of the experiment was not of interest. An alpha level of 0.05 was used to determine significance.

Results

Germination, dormancy, and decomposition rates

Germination rates of *M. vimineum* seed were in general quite high. In the October retrieval at the end of the first growing season, mean germination in the bags buried in 2007 was 56.3 ± 9.3 with a range of 5 to 98%. For the bags buried in 2008, mean germination in the October 2009 retrieval was higher, 79.3 ± 7.9 %, with values ranging from 31 to 99% (Figure 4.1). In both years, mean germination in the roadside environment by the end of the first year was at least 15 percentage points higher than in the other two environments. However, due to the variable nature of the data the differences between environments was not significant at any one sampling point.

Germination occurred throughout the growing season, although most occurred in the first part of the season. In the 2007 burial, nearly half the seeds ($47.7 \pm 15.4\%$)

in the June 2008 retrieval had germinated; in the 2008 burial, $78.7 \pm 5.0\%$ of the seeds in the first June retrieval were germinated.

Loss of seeds to decomposition was quite low; only 3.7% of the seeds throughout the study died without germinating. Among the bags buried in 2007, the highest decomposition rate observed was in the June 2010 retrieval: $11.11 \pm 5.0\%$, not significantly different from the $8.9 \pm 4.9\%$ observed in the October 2010 retrieval. Loss to decomposition was initially higher in the bags of the second start year, but by the time of the second October retrieval the percent of decomposed seeds was similar between the two start years: $4.1 \pm 1.9\%$ for bags buried in 2007 and 6.4 ± 2.6 for bags buried in 2008. Seed bank decay rates in the roadside environment also appeared to be higher: in bags retrieved from the roadside in October 2010, no seeds from the first start and only one seed from the second start were found to be viable (Figure 4.2).

Tetrazolium testing

All of the visual assessments of the seeds I tested in October 2010 by tetrazolium staining were confirmed to be correct.

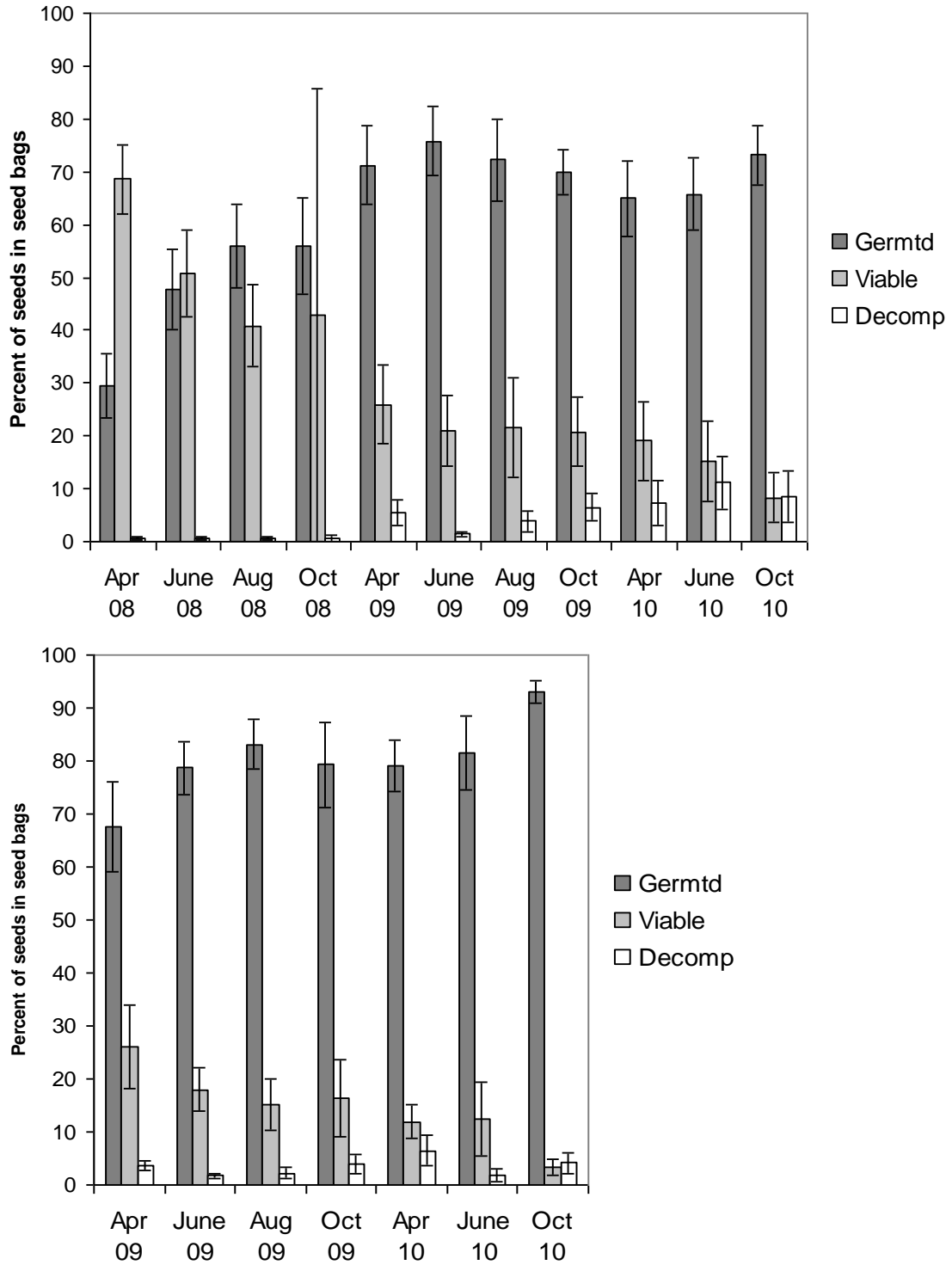


Figure 4.1. Percent of seeds in seed bags (pooled across environments) which were classified as germinated, viable, and decomposed. Top panel shows results from 2007 burial; lower panel shows 2008 burial.

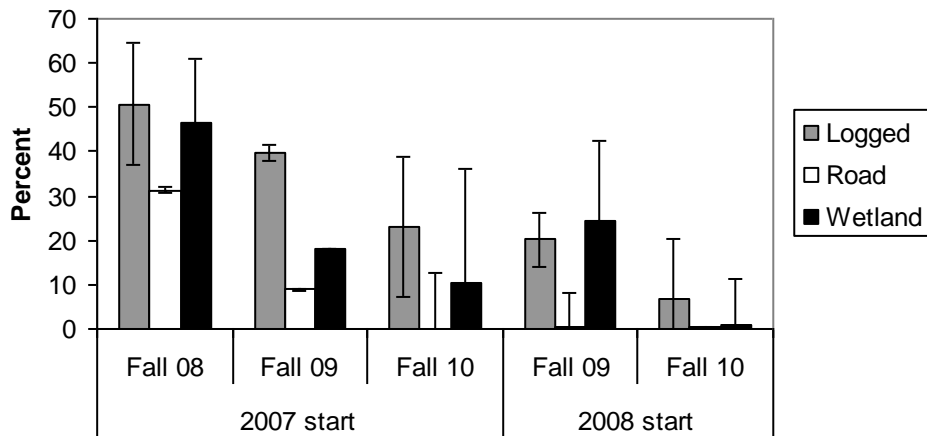


Figure 4.2. Percent of seeds remaining ungerminated and presumed viable after 1, 2, and 3 years of burial (mean \pm se). Note that the mean for wetland sites in fall 2009, 2007 burial, has no associated error bars because it only represents one value.

	numDF	denDF	F-value	p-value
YAB	1	173	57.4752	<.0001
YAB * env	2	173	13.3172	<.0001
YAB * start yr	1	173	33.1603	<.0001

Table 4.1. Analysis of variance of linear mixed effects model for number of dormant seeds in the seed bags. YAB = time of seed bag residence in soil prior to retrieval, entered as years after burial; env = environment type (logged forest, roadside, or wetland); start year has two levels, 2007 start and 2008 start.

Seed bank decay

Analysis of variance of the linear mixed effects model shows that both time since burial (YAB), the interaction of YAB and environment type (estimate of slope by environment type), the interaction of YAB and start year (estimate of slope by start year) are all significant. Table 2 shows the estimates of these slopes, which are actually estimates of the decay parameter k in each environment and start year.

Decay parameters were higher for the data from bags buried in 2008 than from those

buried in 2007. Decay parameters were highest in the roadside and lowest in the wetland environment. The fit of the curves generated from these parameters to the data is shown in Figure 4.3.

	2007	2008
Logged	0.3571	1.5684
Roadside	1.6313	2.8426
Wetland	0.9317	2.1429

Table 4.2. Estimates of exponential decay parameter k for each environment in each start year.

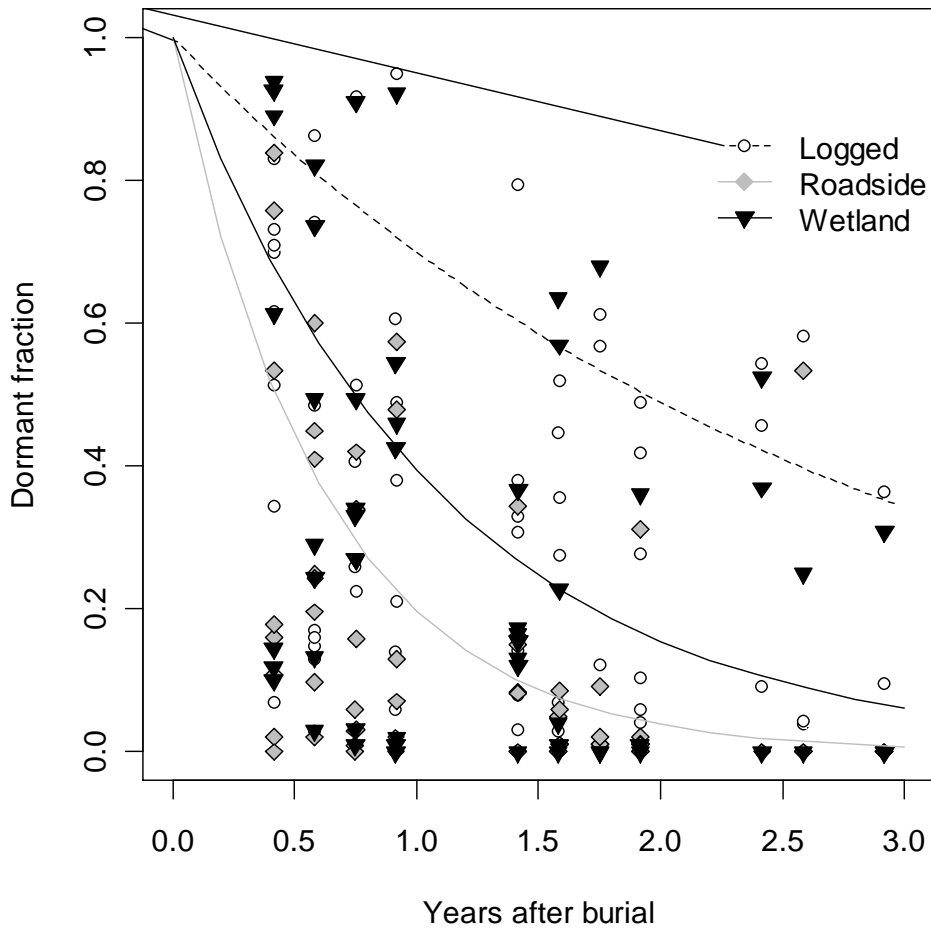


Figure 4.3. Seed bank decay curves and data for each environment for 2007 entry, plotted using decay parameters (k values) estimated by linear mixed effects model.

Discussion

This study demonstrates that *M. vimineum* seed is capable of remaining viable in the soil for two and a half years in the roadside environment, and at least three years in the logged and wetland environments. In having little to no persistence in the seed bank beyond a few years, this species is similar to other weedy summer annual grasses such as quackgrass (*Elytrigia repens*), giant foxtail (*Setaria faberi*), and woolly cupgrass (*Eriochloa villosa*) (Buhler and Hartzler 2001; Conn et al. 2006).

These results are consistent with estimates in the literature of *M. vimineum* seed bank persistence of 3-5 years, based on years of re-emergence throughout consecutive years of herbicide application to prevent seed production (Barden 1987, Tu 2000).

This study shows that *M. vimineum* seedbanks are less persistent in the roadside environment than in the logged and wetland environments. The wetland environment had higher decay constants than the logged environment, which is consistent with other reports that increased soil moisture can result in higher seed decay rates because the wetter environment is more favorable to microbial growth (Chambers and Macmahon 1994). However, the accelerated loss of seeds from the dormant seed bank in the roadside environment seems to be largely a function of the higher initial germination rates there.

Seed bank decay rates were also different between start years. The difference in germination rates in the first year accounted for a large measure of this variation between years. Mean germination in the first year across all environments was much higher for the second start than for the first. Given that most seeds were lost to germination and not decay, it is likely that events regulating germination vary in important ways affecting the proportion of seeds remaining in an ungerminated state.

Van Mourik et al. (2005) suggest that buried seed bag studies can overestimate seed mortality. The mechanism proposed is that buried seed bag studies often utilize bags filled with artificially high densities of seeds, thus exacerbating seed losses due to fungal attack and the artificially high rates of seed-to-seed pathogen transfer. However, this seed density of 100 seeds in 25 cm² bags,

equivalent to 40,000 seeds m^{-1} , is well below seed production estimated for these environments (between 114,740 and 400,480 seeds m^{-2} ; see Chapter 3); it is unlikely that density-dependent seed losses played a role in these results. Rather, it is likely that this buried seed study underestimates seed mortality. All seeds in this study remained under the surface of the soil for the duration of the experiment. However, seeds which remain above the surface of the soil exhibit increased mortality compared to those which are buried beneath the surface (Chauhan et al. 2006; Lutman et al. 2002; Mohler 1993). The environments in this study do not experience significant soil disturbance which would result in the burial of *M. vimineum* seeds. In addition, enclosing the seed in a mesh bags limits access by macroscopic arthropods, organisms known to be important in weed seed predation in agricultural fields (Ward et al. 2011). When seed persistence data from this study was incorporated into a matrix population model and the output of the model compared with field data, it was evident that life stage transition rates derived from this data significantly underestimated seed mortality based on re-emergence data collected on plots in these environments when seed production was prevented for three consecutive years. The model parameterization work indicated that the underestimation was greater for the logged and wetland environments than for the roadside environment; indeed, it is the roadside environment which shows the greatest rate of decay here.

While it is evident that *M. vimineum* seeds which remain above the surface of the soil likely experience higher mortality than what is reflected in the data from these seed bags, it is also possible that disturbances which bury the seeds more deeply might increase seedbank persistence. Burnside et al. (1996) found that increasing depth of burial tended to increase longevity of the seeds of weedy grasses. More work is necessary to elucidate the response of *M. vimineum* seeds to deeper burial, as this could have management implications in environments where soil disturbance makes burial of seeds likely.

These findings imply that *M. vimineum* populations in the roadside environment would be more easily managed than those in the other environments due to their lower seedbank persistence. While the roadside environment is not generally considered to be of conservation interest, it does act as a dispersal corridor for

propagules of invasive plants. Results from this work could help guide the design of management strategies where the frequency of management is matched to the persistence of populations in the seedbank. Management of invasives such as *M. vimineum* on the roadsides could prevent spread into more ecologically sensitive areas where suppression may be more difficult.

Literature Cited

- Anderson RL. 2005. A multi-tactic approach to manage weed population dynamics in crop rotations. *Agronomy Journal* 97: 1579-1583
- Baiser, B., J. L. Lockwood, D. La Puma, and M. F. J. Aronson. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. *Biological Invasions* 10: 785-795.
- Barden LS. 1987. Invasion of *Microstegium vimineum* (Poaceae), an exotic, annual, shade-tolerant, C4 grass, into a North Carolina floodplain. *American Midland Naturalist* 118: 40-45
- Baskin CC and Baskin JM. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego
- Buhler DD and Hartzler RG. 2001. Emergence and persistence of seed of velvetleaf, common waterhemp, woolly cupgrass, and giant foxtail. *Weed Science* 49: 230-235
- Burnside OC, Wilson RG, Weisberg S and Hubbard KG. 1996. Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. *Weed Science* 44: 74-86
- Cacho OJ, Spring D, Pheloung P and Hester S. 2006. Evaluating the feasibility of eradicating an invasion. *Biological Invasions* 8: 903-917
- Chambers JC and Macmahon JA. 1994. A day in the life of a seed - movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* 25: 263-292
- Chauhan BS, Gill G and Preston C. 2006. Influence of environmental factors on seed germination and seedling emergence of rigid ryegrass (*Lolium rigidum*). *Weed Science* 54: 1004-1012
- Claridge, K., and S. B. Franklin. 2002. Compensation and plasticity in an invasive plant species. *Biological Invasions* 4: 339-347.
- Cole PG and Weltzin JF. 2004. Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeastern Naturalist* 3: 545-562
- Conn JS, Beattie KL and Blanchard A. 2006. Seed viability and dormancy of 17 weed species after 19.7 years of burial in Alaska. *Weed Science* 54: 464-470
- Davis AS, Schutte BJ, Iannuzzi J and Renner KA. 2008. Chemical and physical defense of weed seeds in relation to soil seedbank persistence. *Weed Science* 56: 676-684
- DeMeester, J. E., and D. B. Richter. 2010. Differences in wetland nitrogen cycling between the invasive grass *Microstegium vimineum* and a diverse plant community. *Ecological Applications* 20: 609-619.

- Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11: 1287-1300
- Flory SL. 2009. Management of *Microstegium vimineum* invasions and recovery of resident plant communities. *Restoration Ecology* 18: 103-112
- Grabe DF. 1970. *Tetrazolium Testing Handbook for Agricultural Seeds*. Association of Official Seed Analysts, Ithaca, NY, 62 pp
- Judge CA. 2005. Japanese stiltgrass (*Microstegium vimineum*): Population dynamics and management for restoration of native plant communities, Horticultural Science, North Carolina State University, Raleigh, 167 pp
- Lutman PJW, Cussans GW, Wright KJ, Wilson BJ, Wright GM and Lawson HM. 2002. The persistence of seeds of 16 weed species over six years in two arable fields. *Weed Research* 42: 231-241
- Mohler CL. 1993. A model of the effects of tillage on emergence of weed seedlings. *Ecological Applications* 3: 53-73
- Oswalt, C. M., S. N. Oswalt, and W. K. Clatterbuck. 2007. Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *Forest Ecology and Management* 242:727-732.
- Panetta FD. 2007. Evaluation of weed eradication programs: containment and extirpation. *Diversity and Distributions* 13: 33-41
- Pinheiro, J, D. Bates, S. DebRoy, D. Sarkar and the R Core team. 2009. nlme: Linear and nonlinear mixed effects models. R package version 3.1-93.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Redman, D.E. 1995. Distribution and habitat types for Nepal microstegium [*Microstegium vimineum* (Trin.) Camus] in Maryland and the District of Columbia *Castanea* 60: 270-275.
- Schutte BJ, Davis AS, Renner KA and Cardina J. 2008. Maternal and burial environment effects on seed mortality of velvetleaf (*Abutilon theophrasti*) and giant foxtail (*Setaria faberi*). *Weed Science* 56: 834-840
- Simpson GM. 1990. *Seed Dormancy in Grasses*. Cambridge University Press, Cambridge, UK, 297 pp.
- Teo-Sherrell CPA and Mortensen DA 2000. Fates of buried *Sorghum bicolor* ssp *drummondii* seed. *Weed Science* 48: 549-554
- Tu, M. 2000. Elemental Stewardship Abstract for *Microstegium vimineum*. The Nature Conservancy, Arlington, VA.

Van Mourik TA, Stomph TJ and Murdoch AJ. 2005. Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. *Journal of Applied Ecology* 42: 299-305

Ward, MJ, MR Ryan, WS Curran, DA Mortensen, and ME Barbercheck. 2011. Cover crops and disturbance influence activity-density of *Amara aenea* and *Harpalus pensylvanicus* (Coleopetera: Carabidae). *Weed Science* 59: 76-81

Washitani, I. 1985. Field fate of *Amaranthus patulus* seeds subjected to leaf-canopy inhibition of germination. *Oecologia* 66: 338-342

Chapter 5

Modeling suppression and biological control of *Microstegium vimineum* in different environments

Abstract

The control of invasive species presents a significant challenge. Matrix population models are often used to evaluate suppression strategies and the response of invasive plants to biological control agents. I used field data to parameterize matrix models representing populations of the invasive annual grass *Microstegium vimineum* in post-logging, roadside, and wetland environments. I tested whether population responses of *M. vimineum* to management differed by environmental context, and evaluated the biocontrol potential of a fungal pathogen. Modeled suppression events consisted of reducing fecundity by 99% or 100%; the pathogen reduced fecundity by 40% in 80% of the population. As the seedbank is less persistent in the roadside, completely suppressing fecundity for three years extirpated *M. vimineum* in that environment but not the other two. Suppressing fecundity by 99% in every second year caused population to decline over time in all three environments. Neither suppression in every third year nor the pathogen alone was sufficient to cause *M. vimineum* populations to decline, but the combination of the two strategies did cause decline. We conclude that the presence of the pathogen makes it possible to suppress *M. vimineum* with less frequent herbicide applications. Furthermore, the higher tractability of *M. vimineum* populations in the roadside environment could be taken into account in planning buffer zones around ecologically sensitive areas, where exclusion of *M. vimineum* is desired.

Introduction

The control of invasive species presents a significant challenge. Land managers seeking to reduce the adverse ecological impacts of invasive plants may attempt to suppress their populations; however, lack of information about population dynamics, particularly in the seed bank, may hinder control efforts (Panetta 2004).

Further constraints on management include limited resources and concerns about non-target effects (Randall 1996, Blossey 1999). There is also concern that overuse of herbicides in control programs could result in the development of resistant genotypes (Franks et al. 2004, Sterling et al. 2004). Thus the development of management programs which minimize use of resources and chemical inputs while maximizing suppression is very desirable.

Matrix population models can be useful tools for designing and evaluating suppression strategies for invasive species. These models make it possible to identify invasive plant life stages that strongly influence population growth rates, simulate various control scenarios, and project population responses over long periods of time. For example, Hansen (2007) used matrix models to project the response of the invasive grass *Agropyron cristatum* to mechanical and chemical management strategies.

Another frequent use of matrix models is to predict the response of invasive plants to biological control agents. Biological control is often seen as an attractive approach to managing plant invasions, due to the cost and potential ecological impacts of chemical and mechanical control programs (Culliney 2005). Matrix models can address questions such as potential impact of a particular biological control agent (e.g. Shea and Kelly 1998, Schutzenhofer and Knight 2007), or identifying the life stage most important to population growth to guide selection of an agent that will target that stage (Davis et al. 2006). Potential problems with biological control of invasives, however, include non-target effects (Simberloff and Stiling 1996). The use of plant pathogens raises the possibility of invasive plants evolving resistance to the control agent, particularly since genetic variability of the control agents are usually limited due to concerns about host specificity (Myers and Bazely 2003).

Demographic parameters of plant populations can vary due to environmental conditions (Kalisz and McPeck 1992, Buckley et al. 2003), potentially altering the contributions of different life history stages to population growth. When this occurs in invasive plants, these differences can have important implications for management. For example, Shea et al. (2005) used matrix models to demonstrate that differential

success in biological control of *Carduus nutans* among geographical areas could be explained by differences in *C. nutans* population dynamics between invaded areas. Fecundity was more important in New Zealand populations while rosette survivorship was more important in Australian populations; thus biological control agents which target specific life stages would not be equally effective in both of these regions. Working with the invasive grass *Agropyron cristatum*, Hanson and Wilson (2006) modeled population growth rates under different moisture regimes and found that this resulted in differences in population growth parameters. They concluded that herbicide applications may be less effective on populations undergoing rapid growth in wetter environments.

Microstegium vimineum (Japanese stiltgrass) is a widespread invasive grass in the eastern US. It is found in a wide variety of environments (Redman 1995, Cole and Weltzin 2004), and its population growth can be affected by its environmental context (Nord et al. 2010). Its spatial spread in different environments has been modeled; differences in reproductive ratios were found in some but not all years analyzed (Rauschert et al. 2010). I created a population model for *Microstegium vimineum*, parameterizing the model with data collected in central Pennsylvania. The model was then used to quantify the effects of suppression scenarios on *M. vimineum* population growth rates, finding whether demographic parameters vary between *M. vimineum* populations in different environments, and testing whether population responses of *M. vimineum* to management are projected to differ by environmental context. I also used the model to test the effects of a fungal disease on *M. vimineum* populations to evaluate its potential as a biological control agent.

Methods

Study Species

Microstegium vimineum (Trin.) A. Camus (Japanese stiltgrass) is an annual grass of Asian origin which has been expanding its range in the eastern United States since 1919 (Fairbrothers and Gray 1972). Its ability to tolerate a wide range of light and moisture conditions (Winters et al. 1982, Claridge and Franklin 2002, Cole and Weltzin 2004) allow it to invade a wide range of environments including the margins

of forest roads, ditches, stream banks, and wetlands. It also invades forests, particularly following disturbance such as timber harvest (Marshall and Buckley 2008) but also can also spread into intact forests (Cole and Weltzin 2004). Its seeds are dispersed mainly by gravity, water movement, and disturbances such as grading of unpaved roads (Mehrhoff 2000, Rauschert et al. 2010, Mortensen et al. 2010). It is susceptible to a variety of herbicides which can effectively prevent seed production (Judge et al. 2005, Peskin et al. 2005).

In 2009, a disease was discovered in *M. vimineum* populations in West Virginia (Kleczewski and Flory 2010). The pathogen was identified as a member of the genus *Bipolaris*, a blight disease that in a controlled environment study reduced *M. vimineum* inflorescence production by 40%.

Study Sites

M. vimineum demographic data were collected in Rothrock State Forest (Centre County, Pennsylvania), a second-growth oak-hickory forest in central Pennsylvania's ridge and valley physiographic province. *M. vimineum* has been present in the forest for approximately twenty years. Demographic data, including fecundity and population responses to suppression events, were collected at four sites in each of three environments: upland forest which had been logged 5-8 years prior to the start of data collection; wetlands, either slope seeps or saturated areas adjacent to streams, dominated by sedges (*Carex* spp.); and along unpaved limestone gravel roads. See Chapter 3 for more information about sites and data collection. A buried seed bag study carried out at these sites was the source of information about seed fates (see Chapter 4).

Model construction

I constructed an age-structured life cycle diagram to represent the ages seen in late summer prior to seed set (Figure 5.1). Thus, *M. vimineum* individuals were present as reproductive adults or as dormant seeds. I assumed that seeds were no longer viable after remaining dormant through five growing seasons (Tu 2000).

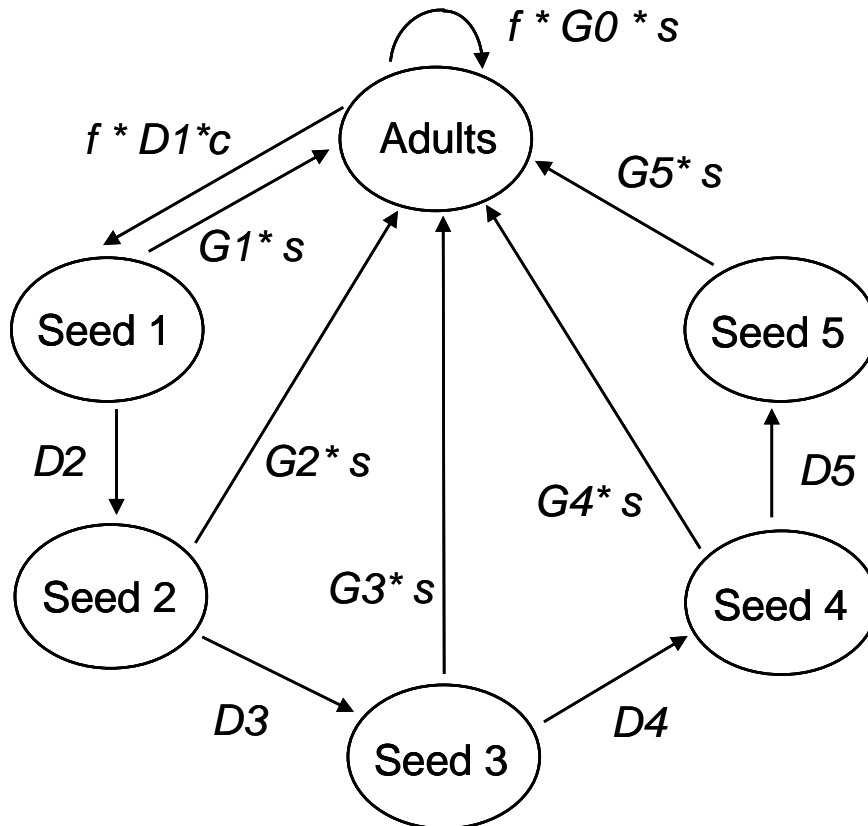


Figure 5.1. Life cycle diagram of *M. vimineum*. The six stages include reproductive adults and an age-structured seedbank with five ages of dormant seeds. Rates labeled G are germination rates. G0 is the germination rate of seeds which do not remain dormant; G1 is the germination rate of seeds which have been dormant through one growing season; and so on. Rates labeled D are probabilities of seeds remaining dormant; f is fecundity; and s is probability of survival from germination to reproduction. The c parameter accounts for mortality of dormant seeds which remain above the soil surface, as this is not reflected in buried seed bag data from which other parameters were derived. Values used for probabilities of transition between stages are given in Table 5.1.

A projection matrix was constructed with each element of the matrix a_{ij} representing the probability of transition from the *ith* to the *jth* stage (Caswell 2001). This matrix is multiplied by a vector whose elements represent the current number of individuals in each stage, in order to project the number of individuals in each stage in the next time step. In this model each time step represents one year.

As germination and dormancy rates vary among the environments (Chapter 4), I parameterized a different projection matrix for each of the three environments. I assumed the same probability of seedling survival and establishment for all environments, 0.25 (Gibson et al. 2002, Schramm and Ehrenfeld 2010).

The parameter c accounts for survivorship on the soil surface. The estimates of survival in the seedbank from Chapter 4 do not account for higher mortality of seed on the surface of the soil (Mohler 1993, Lutman et al. 2002), which may be particularly high in the logged and wetland environments. The physical complexity above the soil surface is greater in the logged and wetland environments than in the roadside environment, where there is less leaf litter and greater chance of seeds contacting soil. Therefore the additional survivorship parameter I applied to the DI transition was higher for the roadside model ($c = 0.8$) than for the other two environments ($c = 0.18$). I estimated this parameter by comparing model output following complete suppression of seed production with data from one start year of the field experiment (Chapter 3). As herbicide application completely prevented seed production, a comparison of model output with the field data facilitated calibration of the seedbank dynamics. After the model was parameterized, its results were compared with adult census data from the second experimental start year for verification (Figure 5.2).

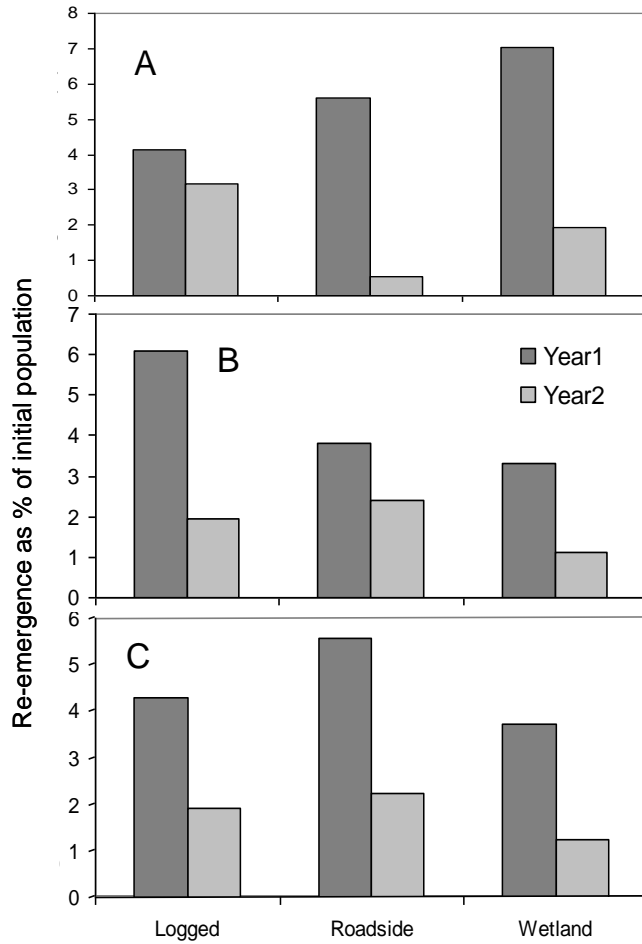


Figure 5.2. Recruitment to adult population pool following complete suppression of seed production, in a) model; b) field data used to parameterize model; and c) field data used to validate model. Data are presented as percent of initial population.

	G0	G1	G2	G3	G4	G5	s
Logged	0.611	0.136	0.165	0.187	0.176	0.176	0.250
Roadside	0.828	0.143	0.051	0	0	0	0.250
Wetland	0.614	0.261	0.269	0.110	0.110	0.110	0.250
	D1	D2	D3	D4	D5	m	
Logged	0.355	0.655	0.545	0.300	0.250	0.180	
Roadside	0.160	0.287	0	0	0	0.8	
Wetland	0.356	0.267	0.545	0.300	0.250	0.180	

Table 5.1. Probabilities used to construct transition matrices for each environment. Refer to Figure 1 for definition of parameters.

Fecundity of *M. vimineum* differs between the three environments, due to differences in biomass achieved by the plants. Average fecundities measured over two years of field observations were 28.0 seeds per plant in the logged environment, 21.8 seeds per plant in the roadside environment, and 33.6 seeds per plant in the wetland environment (A. Nord, unpublished data). I used these parameters as baseline fecundity parameters.

For each projection matrix I calculated the population growth rate λ , the dominant eigenvalue of the matrix (Caswell 2001). When $\lambda < 1$ the population is projected to decline; when $\lambda > 1$ the population is projected to increase. I calculated λ for *M. vimineum* in each environment using the average fecundities observed in the field, and also across a range of fecundities for each environment. I also calculated elasticities, the proportional changes in λ resulting from a change in each population parameter, e.g. *DI*, or lower-level vital rate, e.g. *G1* or *s* (Caswell 2001).

I constructed the model in R version 2.9.2 (The R Development Core Team 2009). Calculations of elasticity and λ for baseline models were performed using the R popbio package version 2.1 (Stubben and Milligan 2007).

Modeling herbicide scenarios

M. vimineum suppression events were simulated by multiplying fecundity *f* by 0.01 in steps specified as “suppression years,” to simulate a herbicide application which reduces seed production by 99%. *M. vimineum* is very sensitive to a variety of herbicides (Peskin 2005, Judge 2005) making this a realistic assumption. In field experiments conducted in the Rothrock State Forest in the modeled environments, seed production was completely prevented by herbicides (Chapter 3).

To compare the duration of effort necessary to eradicate *M. vimineum* populations in the three environments, I began each model run with 10 adult individuals and no dormant seeds, to simulate the effect of a few seeds being transported into a new site and germinating. I let each population grow for nine years, then applied suppression in every subsequent iteration to see how many years of suppression were required until there were no individuals left. This was repeated in each environment across a range of fecundity values from 15 to 55.

As land managers may not have resources to apply suppression measures every year, I also assessed the effectiveness of herbicide application when not applied in consecutive years. I began each model run as described above for nine iterations, then applied suppression in every second year, every third year, and for three consecutive years followed by once every three years. In these scenarios population size peaks in the year preceding application then decreases following application. I calculated an overall λ for each scenario as the equivalent annual growth rate by taking the geometric mean of the λ values at each time step in the growth and suppression cycle, i.e. from one population peak to the next (Wittmer et al. 2007).

Modeling *Bipolaris* infection

Kleczewski and Flory (2010) report that greenhouse-grown *M. vimineum* inoculated with the higher treatment level of *Bipolaris* produced 40% fewer seedheads; the authors believe this to be well within the range of inoculation pressure experienced by plants in the field. I therefore assumed that infection, which affects adult plants, would reduce fecundity by 40%. I represented the proportion of infected *M. vimineum* individuals in a population with the variable i ; thus the parameter f in the models for uninfected populations was replaced by the term $f*(1 - i) + f*(1 - 0.4)*i$ to reflect the seed production of both infected and uninfected individuals. The value of i remained constant within each model run.

To test the effect of the pathogen by itself in populations with varying infection rates, I began with the fecundities observed in the field for each environment and assumed the infection reduced fecundity by 40%. I then calculated λ while varying the proportion of infected individuals i from 1 to 100.

For the herbicide plus pathogen scenarios, I set the proportion of infected *M. viminem* individuals to 80%. In these scenarios I tested two levels of pathogenicity, with seed production suppressed by 40% and by 60%, as Kleczeskwi and Flory (2010) felt that the impact of the pathogen on seed production in the field might well be greater than the 40% reduction observed in the greenhouse.

To test the interaction of the pathogen and herbicide application, I first ran the models for nine iterations to simulate uncontrolled population growth using

fecundities observed in the field. For the next 12 iterations I assumed infection rates in the population of 80%, and applied the herbicide control factor every third year with 99% suppression of seed production. This was repeated with an infection rate of 60 percent.

Results

Population growth rates and elasticity analysis of unsuppressed populations

The rate of population growth (λ) was greater than one for populations in all three environments, indicating a positive rate of growth. At levels of fecundities observed in the field, λ is 4.3 in the logged, 4.6 in the roadside, and 5.23 in the wetland environment.

The vital rates with the highest elasticity, meaning the parameters whose change produces the greatest proportional change in population growth λ , were fecundity and establishment rates, whose elasticity was at least 0.986 in all three environments (Table 5.2). However, the elasticity for the rate of germination of new seeds was nearly as high. Elasticities of all other parameters were extremely low.

	Logged	Roadside	Wetland		Logged	Roadside	Wetland
f	0.9884	0.9876	0.9859	G0	0.9786	0.9755	0.9725
est	0.9884	0.9876	0.9859	G1	0.0080	0.0118	0.0127
m	0.0097	0.0121	0.0134	G2	0.0015	0.0003	0.0007
D2	0.0017	0.0003	0.0007	G3	0.0002	0	0.0000
D3	0.0002	0	0.0000	G4	0.0000	0	0.0000
D4	0.0000	0	0.0000	G5	0.0000	0	0.0000
D5	0.0000	0	0.0000	D1	0.0097	0.0121	0.0134

Table 5.2. Elasticities of vital rates and parameters. Fecundities used were those observed in the field: 28.0 in the logged, 21.8 in the roadside, and 33.6 in the wetland environment.

Effect of herbicide application

At the lowest fecundity I tested (15 seeds per plant), it took five years of suppression (seed production reduced by 99%) to extirpate the population in the roadside environment, but eight years in the logged environment (Figure 5.3). Years to extirpation was consistently lower in the roadside environment than in the other two at any one given fecundity. At the average fecundities observed in the field (28.0 seeds per plant in the logged environment, 21.8 in the roadside, and 33.6 in the wetland environments), predicted time to extirpation is 11 years for the logged, 12 for the wetland, and 7 for the roadside environment.

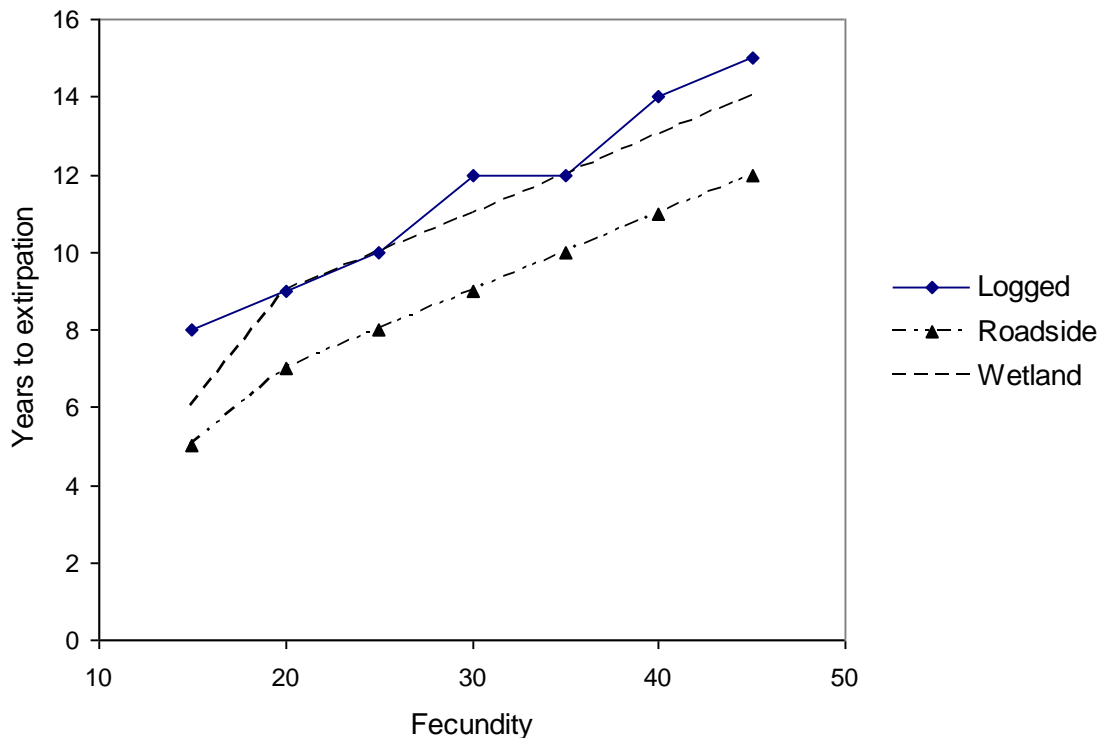


Figure 5.3. Years to extirpation as a function of fecundity in the three environments. This assumes a control efficacy of 99% reduction in seed production, with control applied every year following nine years of initial unsuppressed population growth.

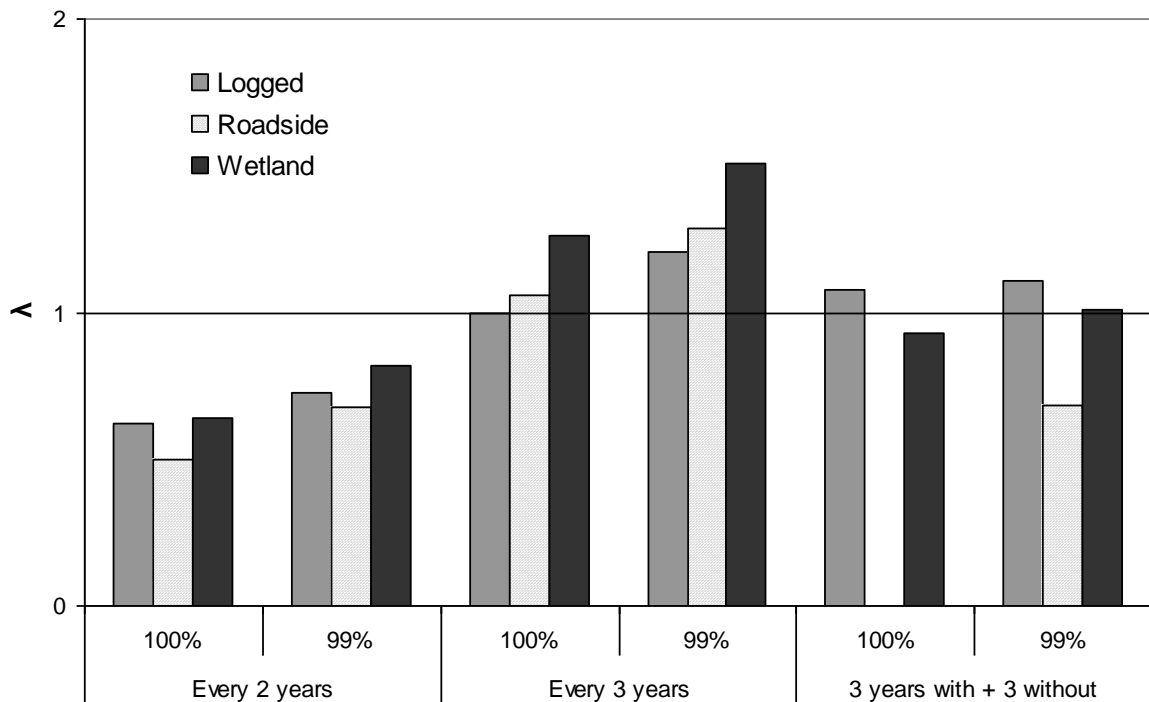


Figure 5.4. Values of λ for 3 suppression cycles at two efficacy rates in each environment. The suppression cycles represent herbicide application once every two years, once every three years, and a cycle of three years with herbicide application followed by three years without. Efficacy rates represent 100% suppression of seed production (no seeds produced) and 99% suppression of seed production (1% of potential fecundity realized).

When suppression events occurred every other year, populations in all environments declined ($\lambda < 1$) when the models used fecundity levels observed in the field (Figure 5.4). With this suppression frequency at an efficacy of 99% prevention of seed production, fecundity levels would have to exceed 49 seeds per plant for logged, 36.5 for roadside, and 44.7 for wetland environments in order for λ to exceed 1 under this suppression scenario. This represents fecundity increases of 75%, 64%, and 33%, respectively. In order to keep $\lambda < 1$ with application every two years, suppression must reduce seed production by at least 96.2% in the logged, 96.4% in roadside, and 97.8% in the wetland environment.

In contrast, if the suppression events occurred every three years, populations in all environments increased ($\lambda > 1$) at both 99% and 100% prevention of seed production. Fecundity levels had to be set no higher than 21.4 seeds per plant in logged, 15.9 in roadside, and 19.1 in wetland environments in order to obtain $\lambda < 1$.

The scenario of herbicide application for three years followed by three years without application was more sensitive to level of seed suppression achieved. If all seed production was prevented for three years, *M. vimineum* was extirpated from the roadside environment because the seed bank in that environment is less persistent. Neither efficacy level modeled (99% or 100% prevention of seed production) was sufficient to achieve $\lambda < 1$ in the logged environment; in the wetland environment, $\lambda < 1$ only when seed production was completely prevented.

Effect of *Bipolaris* infection

The effect of the *Bipolaris* pathogen by itself, assuming that infected plants produced only 60% as many seeds as uninfected plants, was not sufficient to reduce λ to less than 1 in any environment, regardless of what proportion of *M. vimineum* individuals within the populations were infected (Figure 5.5). λ values were as high as 4.9 in the wetland environment with no infection. Even with 100% of individuals infected, λ never fell below 2.5.

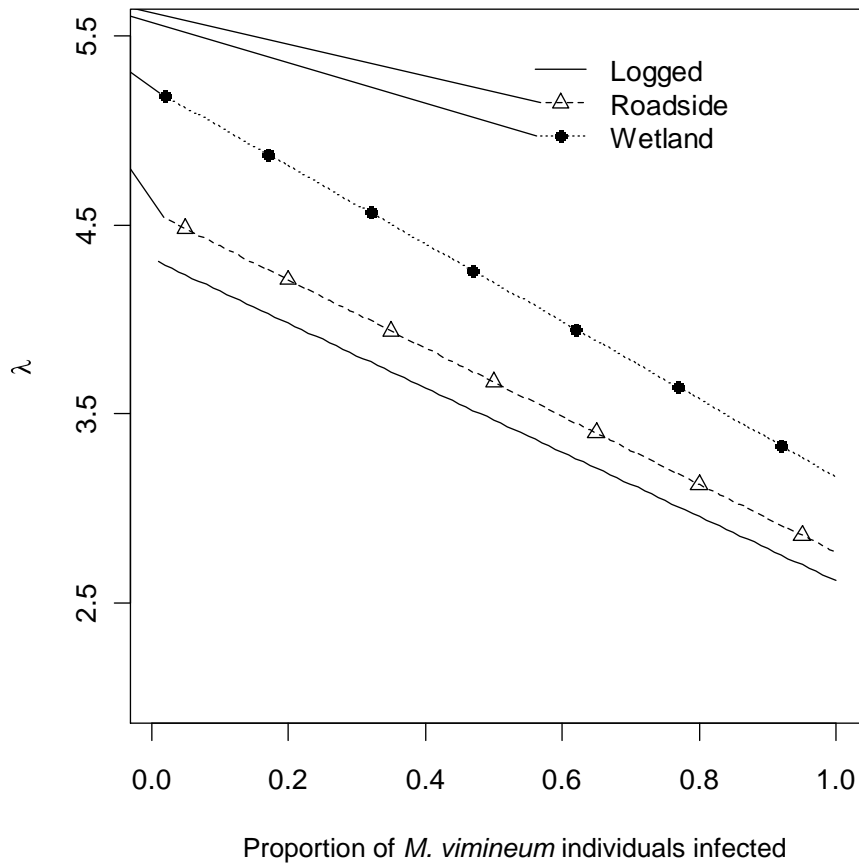


Figure 5.5. Response of λ to varying rates of *M. vimineum* individuals infected with the *Bipolaris* pathogen in three environments.

When 80% of the *M. vimineum* population was infected with *Bipolaris*, herbicide applications in every third year were sufficient to achieve $\lambda < 1$ in the logged and roadside environments (Figure 5.6). In the wetland environment, this infection rate and application scenario lowered λ only to 1.13, not enough to suppress the population over time. An infection rate of 50% combined with herbicide in every third year, however, was not sufficient to cause population decline in any environment. An infection rate of 80%, with seed set reduction of infected plants increased 60%, led to λ between 2 and 3 in all environments, but when combined with herbicide every three years $\lambda < 1$ in all environments (Table 5.3).

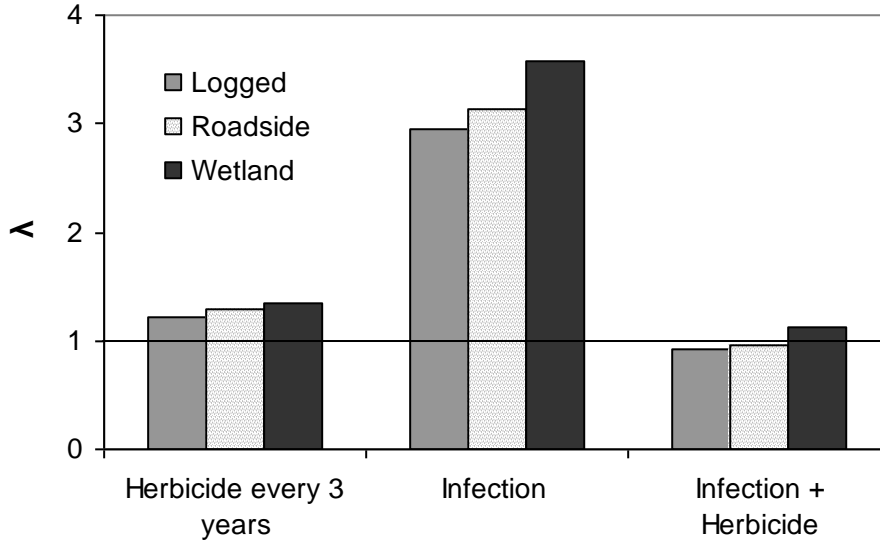


Figure 5.6. Response of λ in *M. vimineum* populations in three environments to herbicide application every 3 years with 99% reduction of seed production; infection of 80% of population every year by pathogen which reduces seed production by 40%; and combination of herbicide regime and infection.

Scenario	Rate of seed suppression by herbicide	Rate of seed suppression by infection	Infection rate in MIVI population	λ values		
				Logged	Roadside	Wetland
Herbicide every 2nd year	100%			0.620	0.501	0.642
Herbicide every 2nd year	99%			0.724	0.678	0.819
Herbicide every 3rd year	100%			0.996	1.057	1.264
Herbicide every 3rd year	99%			1.209	1.285	1.506
3 years herbicide + 3	100%			1.079	0.000	0.931
3 years herbicide + 3	99%			1.106	0.685	1.012
Infection		40%	80%	2.956	3.126	3.577
Infection		60%	80%	2.275	2.404	2.754
Infection + Herbicide every	99%	40%	80%	0.926	0.950	1.127
Infection + Herbicide every	99%	60%	80%	0.787	0.776	0.931

Table 5.3. Summary of λ values from modeled *M. vimineum* suppression scenarios, including parameter settings used in model scenarios.

Discussion

The models of unsuppressed *M. vimineum* populations project rapid growth in all environments, as all λ values were at least 4.3. *M. vimineum* population parameters did differ somewhat between environments. Seed bank dynamics especially differed between the roadside and the other two environments: in the roadside, no seeds survived beyond two growing seasons of dormancy. Germination of new seeds was greater in the roadside leaving fewer seeds to enter the dormant seed bank. λ of unsuppressed populations was lowest in the logged environment although still greater than 1, indicating growing populations. Logged environment germination rates of new seeds and transition of seeds into the dormant seed bank were almost the same as those of the wetland environment, but germination rates of seeds out of the dormant seed bank were lower.

Analysis of the parameters showed that the elasticity of the fecundity parameter is very high. The primary population-level effects of the suppression strategies I used in the model, herbicide and fungal pathogen, are the reduction or prevention seed production; the elasticity analysis confirms that these strategies are appropriate for this species and likely to be effective.

The modeled herbicide scenarios showed that by suppressing 99% of seed production, it was possible to drive populations to extirpation in 7-12 years. In all environments, application in every second year was sufficient to keep populations in decline. While fecundity might be expected to vary from year to year depending on factors such as precipitation (Gibson et al. 2002, Webster et al. 2008), increases of the magnitude needed to overwhelm this suppression scenario are unlikely. Nor is it likely that environmental conditions would result in fecundities low enough to prevent population growth in the scenario of herbicide application every second year (λ values for this scenario ranged from 1.2 to 1.5), unless perhaps coupled with some other management technique such as mowing.

In general, population dynamics of *M. vimineum* were not sufficiently different between the three environments to result in large differences in the populations' response to modeled suppression in the absence of the pathogen. In these models the importance of the seed bank parameters to population growth was

overshadowed by that of fecundity. While there were some differences in fecundity between the environments as measured in the field, these differences were not large enough to result in substantially different responses to management. The one exception is the scenario of three years of completely preventing seed production, which was enough to deplete the seed bank and extirpate the population in the roadside environment, but not in the other two

The reduced seed bank persistence in the roadside environment did result in a lower prediction of years of suppression effort required for extirpation. However, the model assumes no seed dispersal from other populations. This may not be a valid assumption for this environment, as the road may be acting as a dispersal corridor (Christen and Matlack 2009; Mortensen et al. 2010).

Although the modeled *Bipolaris* infection was not enough to suppress *M. vimineum* populations, the combination of the pathogen and herbicide application in every third year did force *M. vimineum* populations to decline in two of the three environments. Thus, even if the pathogen itself cannot provide adequate *M. vimineum* suppression, it does reduce the amount of management effort required to achieve satisfactory control. In the wetland environment, higher baseline fecundity coupled with slightly higher germination rates from the dormant seed bank kept the pathogen from having enough impact to make a 3-year herbicide application interval effective. It is possible that the rate of 40% reduction in seed production is low compared to what might occur in the field; Kleczewski and Flory (2010) observed some populations in which the impact of the pathogen was great enough to cause mortality of *M. vimineum* individuals. More field data describing the pathogenicity of this organism is needed to better model probable population-level responses.

The interactions of *Bipolaris* and herbicide control are potentially more complex than modeled here. Herbicide applications could reduce *M. vimineum* populations to a low enough level that *Bipolaris* population is reduced, resulting in a lag of *M. vimineum* suppression until the pathogen populations rebuild. It is also possible that the herbicide could directly affect either the growth of the pathogen or the susceptibility of its host (Agrios 1997). If the pathogen makes the plants more susceptible to herbicides so that lower rates could be used, or has a thinning effect on

dense populations that improves herbicide contact on all plants, their effect could be synergistic: the combined effect could be greater than the sum of both individual effect. Synergism has been explored for weed suppression in agronomic systems (Ryan et al. 2011, Teasdale et al. 2005); the possibility of synergism between tactics of invasive plant suppression perhaps merits further attention.

It is very possible that the influence of the environmental context on *M. vimineum* would be greater in models including population dynamics of the pathogen. For example, Kleczewski and Flory (2010) propose that the spores of the pathogen overwinter in thatch. *M. vimineum* plants tend to be smaller and occur at lower densities along the roadside (Chapter 3); this would result in lower thatch accumulation providing reduced overwintering refugia for the fungus. The higher moisture present in the wetland environment could increase germination and growth of the pathogen; in general more humid conditions favor fungal pathogens (Agrios 1997). Furthermore, *M. vimineum* plants in the roadside environment have high foliar concentrations of calcium (Chapter 2); this could increase their resistance to fungal pathogens (Agrios 1997).

These models show that suppression of *M. vimineum* populations is feasible even when herbicides are not applied every year. Even though populations may rebound somewhat in the interval between applications, over time populations decline if the intervals are not too long. The presence of the *Bipolaris* pathogen makes it possible to lengthen the intervals between herbicide application. This would reduce the cost of management as well as the ecological risks of frequent herbicide use. Such a combination of strategies could also reduce the risk that the target species would develop resistance to either the herbicide or the pathogen, as selection pressures exerted by management would vary from year to year.

Literature Cited

- Agrios, G. 1997. Plant Pathology. 4th ed. edition. Academic Press, San Diego, CA.
- Blossey, B. 1999. Before, during and after: the need for long-term monitoring in invasive plant management. *Biological Invasions* 1: 301-311.
- Buckley, Y. M., D. T. Briese, and M. Rees. 2003. Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *Journal of Applied Ecology* 40: 481-493.
- Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. 2nd edition. Sinauer Associates, Inc., Sunderland, MA.
- Christen, D. C., and G. R. Matlack. 2009. The habitat and conduit functions of roads in the spread of three invasive plant species. *Biological Invasions* 11: 453-465.
- Claridge, K., and S. B. Franklin. 2002. Compensation and plasticity in an invasive plant species. *Biological Invasions* 4: 339-347.
- Cole, P. G., and J. F. Weltzin. 2004. Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeastern Naturalist* 3: 545-562.
- Culliney, T. W. 2005. Benefits of classical biological control for managing invasive plants. *Critical Reviews in Plant Sciences* 24: 131-150.
- Davis, A. S., D. A. Landis, V. Nuzzo, B. Blossey, E. Gerber, and H. L. Hinz. 2006. Demographic models inform selection of biocontrol agents for garlic mustard (*Alliaria petiolata*). *Ecological Applications* 16: 2399-2410.
- Fairbrothers, D. E., and J. R. Gray. 1972. *Microstegium vimineum* (Trin.) A. Camus (Gramineae) in the United States. *Bulletin of the Torrey Botanical Club* 99: 97-100.
- Franks, S. J., P. D. Pratt, F. A. Dray, and E. L. Simms. 2004. Selection for resistance in invasive plants. *Weed Technology* 18: 1486-1489.
- Gibson, D. J., G. Spyreas, and J. Benedict. 2002. Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. *Journal of the Torrey Botanical Society* 129: 207-219.
- Hansen, M. J. 2007. Evaluating management strategies and recovery of an invasive grass (*Agropyron cristatum*) using matrix population models. *Biological Conservation* 140: 91-99.
- Hansen, M. J., and S. D. Wilson. 2006. Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? *Journal of Applied Ecology* 43: 269-280.
- Judge, C. A., J. C. Neal, and J. F. Derr. 2005. Response of Japanese stiltgrass (*Microstegium vimineum*) to application timing, rate, and frequency of postemergence herbicides. *Weed Technology* 19: 912-917.

- Kalish, S., and M. A. McPeck. 1992. Demography of an age-structured annual - resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology* 73: 1082-1093.
- Kleczewski, N. M., and S. L. Flory. 2010. Leaf blight disease on the invasive grass *Microstegium vimineum* caused by a *Bipolaris* sp. *Plant Disease* 94: 807-811.
- Lutman, P. J. W., G. W. Cussans, K. J. Wright, B. J. Wilson, G. M. Wright, and H. M. Lawson. 2002. The persistence of seeds of 16 weed species over six years in two arable fields. *Weed Research* 42:231-241.
- Marshall, J. M., and D. S. Buckley. 2008. Effects of microsites created by selective harvesting on growth of *Microstegium vimineum* in a central hardwood forest. *Forest Science* 54:534-542.
- Mehrhoff, L. J. 2000. Perennial *Microstegium vimineum* (Poaceae): An apparent misidentification? *Journal of the Torrey Botanical Society* 127:251-254.
- Mortensen, D.A., E.S.J. Rauschert, A.N. Nord, and B.P. Jones. 2009. Forest roads facilitate the spread of invasive plants. *Invasive Plant Science and Management* 2: 191-199.
- Mohler, C. L. 1993. A Model of the Effects of Tillage on Emergence of Weed Seedlings. *Ecological Applications* 3: 53-73.
- Myers, J. H., and D. R. Bazely. 2003. *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge, UK.
- Nord, A. N., D. A. Mortensen, and E. S. J. Rauschert. 2010. Environmental factors influence early population growth of Japanese Stiltgrass (*Microstegium vimineum*). *Invasive Plant Science and Management* 3: 17-25.
- Panetta, F. D. 2004. Seed banks: the bane of the weed eradicator. Pages 523-526 in *Proceedings of the 4th Australian Weeds Conference*. Weed Society of New South Wales, Wagga Wagga, New South Wales.
- Peskin, N., D. A. Mortensen, B. P. Jones, and M. R. Booher. 2005. Grass-selective herbicides improve diversity of sites infested with Japanese stiltgrass (Pennsylvania). *Ecological Restoration* 23: 64-65.
- R Development Core Team 2009. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Randall, J. M. 1996. Weed control for the preservation of biological diversity. *Weed Technology* 10: 370-383.
- Rauschert, E. S. J., D. A. Mortensen, O. N. Bjornstad, A. N. Nord, and N. Peskin. 2010. Slow spread of the aggressive invader, *Microstegium vimineum* (Japanese stiltgrass). *Biological Invasions* 12: 563-579.
- Redman, D. E. 1995. Distribution and habitat types for Nepal microstegium [*Microstegium vimineum* (Trin.) Camus] in Maryland and the District of Columbia. *Castanea* 60: 270-275.

- Ryan, M.R., S.B. Mirsky, D.A. Mortensen, J.R. Teasdale, and W.S. Curran. 2011. Potential synergistic effects of cereal rye biomass and soybean planting density on weed suppression. *Weed Science* 59: 238-246.
- Schramm, J. W., and J. G. Ehrenfeld. 2010. Leaf litter and understory canopy shade limit the establishment, growth and reproduction of *Microstegium vimineum*. *Biological Invasions* 12: 3195-3204.
- Schutzenhofer, M. R., and T. M. Knight. 2007. Population-level effects of augmented herbivory on *Lespedeza cuneata*: Implications for biological control. *Ecological Applications* 17: 965-971.
- Shea, K., and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* 8: 824-832.
- Shea, K., D. Kelly, A. Sheppard, and T. Woodburn. 2005. Context-dependent biological control of an invasive thistle. *Ecology* 86: 3174-3181.
- Simberloff, D., and P. Stiling. 1996. How risky is biological control? *Ecology* 77: 1965-1974.
- Sterling, T. M., D. C. Thompson, and L. B. Abbott. 2004. Implications of invasive plant variation for weed management. *Weed Technology* 18: 1319-1324.
- Stubben, C.J. and Milligan, B.G. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22: 1-23.
- Teasdale, J.R., P. Pillai, and R.T. Collins. 2005. Synergism between cover crop residue and herbicide activity on emergence and early growth of weeds. *Weed Science* 53: 521-527.
- Tu, M. 2000. Element stewardship abstract for *Microstegium vimineum*. The Nature Conservancy, Arlington, VA.
<http://www.imapinvasives.org/GIST/ESA/esapages/documnts/micrvim.pdf> Accessed 4-11-2011.
- Webster, C. R., J. H. Rock, R. E. Froese, and M. A. Jenkins. 2008. Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10-year results. *Oecologia* 157: 497-508.
- Winters, K., M. R. Schmitt, and G. E. Edwards. 1982. *Microstegium vimineum*, a shade adapted C4 [carbon pathway] grass [Comparison of growth with *Digitaria sanguinalis* and *Sporobolus airoides*]. *Plant Science Letters* 24: 311-318.
- Wittmer, H. U., R. A. Powell, and C. M. King. 2007. Understanding contributions of cohort effects to growth rates of fluctuating populations. *Journal of Animal Ecology* 76:946-956.

Epilogue

My thinking about invasive plants has become more nuanced during the process of working on this dissertation. While I found relatively few statistically significant examples of *M. vimineum* responses to habitat types and strong explanatory power in very small-scale variables, I have become more convinced that a serious consideration of invasive plants cannot be separated from a discussion of the broader-scale environmental context. In forests that are fragmented, crisscrossed by extensive road systems, and subject to sometimes intense deer browse, it is perhaps no wonder that plant communities are no longer the same as they were a hundred years ago. This question of whether invasive species are agents or rather merely beneficiaries of ecological change was first addressed in two frequently cited papers: Didham et al. (2005) explored the theoretical underpinnings, and MacDougal and Turkington (2005) tested the hypothesis with manipulative experiments in oak savannah. I am increasingly of the opinion that *M. vimineum* is a “passenger,” a species taking advantage of opportunities offered by the present environment in a way the native species cannot. For example, consider the results of Chapter 2: *M. vimineum* abundance along limestone gravel roads is high. Along shale roads where *M. vimineum* is less abundant, there is not a greater abundance of native (or even less aggressive alien) species. There is simply more area with no plant cover at all.

That said, it still seems to me that there is value in seeking to manage the populations of invasive plants. While they may indeed be “passengers of ecological change” and not necessarily the drivers, once established they are not without ecological impact. The many impacts of *M. vimineum* were discussed in the Prologue; I will not review them here except to note that my findings, particularly the plant community responses to *M. vimineum* suppression detailed in Chapter 3, are consistent with the greater body of literature. *M. vimineum* population success can come at the expense of native species in some circumstances.

In considering what differences may exist in *M. vimineum* responses to control in different environmental contexts, I have become convinced that any differences are largely due to the effect of the site on the actual suppression activity. Mechanical methods are much more difficult in terrain that is very uneven or has a lot of woody

debris; furthermore, the intensity of labor needed for mechanical suppression would realistically limit this approach to small-scale projects in which the risk of non-target effects from chemicals is considered too great. However, attempting to spray herbicide in such a way as to achieve adequate contact with *M. vimineum* foliage, in a setting such as a wet meadow that is also occupied by bushy vegetation such as tall goldenrod (*Solidago canadensis*), has its own set of challenges. Labeling restrictions on herbicide use are also different in upland than in wetland/riparian areas. Meanwhile *M. vimineum* establishes in all these settings; this work has given me a new appreciation for its plasticity and its ability to not only survive but thrive across a wide range of environments.

So how might my work inform management of *M. vimineum*? First, I think it highlights the fact that site-specific constraints on what suppression tactics can be used can have a large impact on final outcomes, both in terms of *M. vimineum* populations and in the response of the surrounding plant community.

My work suggests that infestations of *M. vimineum* are most tractable to management along roadsides. This raises an interesting question: what would be the objective of seeking to manage *M. vimineum* in this environment? The plant communities it competes with here are hardly of conservation value; they consist mostly of other weedy and non-native species, although perhaps not as aggressive as *M. vimineum*. In fact I don't think it particularly pressing to suppress *M. vimineum* along most of the forest road network. It seems to me to be much more important to identify critical areas of the road network which are likely to act as sources from which *M. vimineum* propagules colonize wetlands or zones of timber harvest, and focus suppression efforts there in order to slow the spread of *M. vimineum* into areas where its ecological impact would be far greater. Once *M. vimineum* is present in a wetland options for suppressing it are limited if there is standing water present that precludes the use of grass-specific herbicides; it would seem to be more effective to identify buffer zones around areas like this and seek to keep the buffer zones free of infestation, keeping in mind that roads are a very likely point of entry. If it is decided to take action to suppress *M. vimineum* in an environment like a wetland, I think it is important to consider how re-invasion will be prevented, particularly if the

suppression tactics have left large amounts of ground unvegetated. Any wholistic restoration program will also address the underlying problems which facilitate *M. vimineum* success (Smith et al. 2006).

While I expected to find some differences between limestone and shale gravel roads, the magnitude and spatial extent of the effect of limestone dust on soil chemistry were surprising. It would be interesting to evaluate the impact this effect might have germination and establishment of native forest plants, particularly the acidophilic ericaceous species common in Pennsylvania's forest understory. The spatial distribution of these species that we see today may be a relic of historical (pre-limestone) establishment patterns; as these species are long-lived and clonal, it may be decades before the effect of limestone dust upon the distribution of ericaceous species is fully expressed. This also raises the question of how ecologically sensitive systems might be impacted by limestone dust. While it is unlikely that the use of limestone gravel will be abandoned in road construction, it is worth considering whether short stretches of unpaved roads near particularly sensitive areas should be surfaced with some other material.

M. vimineum is spreading in a context of disturbance. There is arguably not a single place left in Pennsylvania that could be called "pristine:" fragmentation, pollution, and intense deer pressure are a few of the forces shaping today's forests. Invasive plants certainly belong on that list as well, even as these other forces may be facilitating their spread. However, I believe it is possible to mitigate some of the impacts of invasive plants. It is also necessary – our ecosystems may no longer be "pristine" but they are far from worthless. The pressures they face mean that management such as invasive plant suppression is necessary to preserve their value.

Literature Cited

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmill. 2005. Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution* 20:470-474.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42-55.

Smith, R. G., B. D. Maxwell, F. D. Menalled, and L. J. Rew. 2006. Lessons from agriculture may improve the management of invasive plants in wildland systems. *Frontiers in Ecology and the Environment* 4:428-434.

Appendix

Supplementary Figures and Tables

	numDF	denDF	F-value	p-value
Trt	1	191	141.2415	<.0001
Side	1	191	2.31957	0.1294
Trt:Side	1	191	0.05149	0.8207

Table A1. From Chapter 2. Analysis of variance for *M. vimineum* extent away from road, testing differences between road types and side (upslope/downslope). (n=198)

Year	Type	Intercept	St.Err Int	Slope	St.Err Slope	Adj. R-sq
2007	stems	-0.02967	0.03803	1.00114	0.03835	0.9315
2007	tillers	0.1383	0.04852	1.04571	0.05457	0.8300
2008	stems	-1.1839	0.3863	1.5293	0.2571	0.7256
2008	tillers	0.22954	0.11675	1.01648	0.08612	0.8848
2009	stems	-1.40798	0.11069	1.71043	0.07787	0.8908
2009	tillers	0.34152	0.09467	0.78666	0.07988	0.7218

Table A2. From Chapter 3. Linear models of log-transformed seed production as a function of log-transformed stem or tiller length for each year.

	numDF	denDF	F-value	p-value
env	2	21	2.4609	0.1096
trt.yr	1	29	2.4996	0.1247
env:trt.yr	2	29	1.3401	0.2776

Table A2. From Chapter 3. Anova of model for estimates of post-treatment seed production in mechanically-treated plots in all three treatment years, with plot as random.

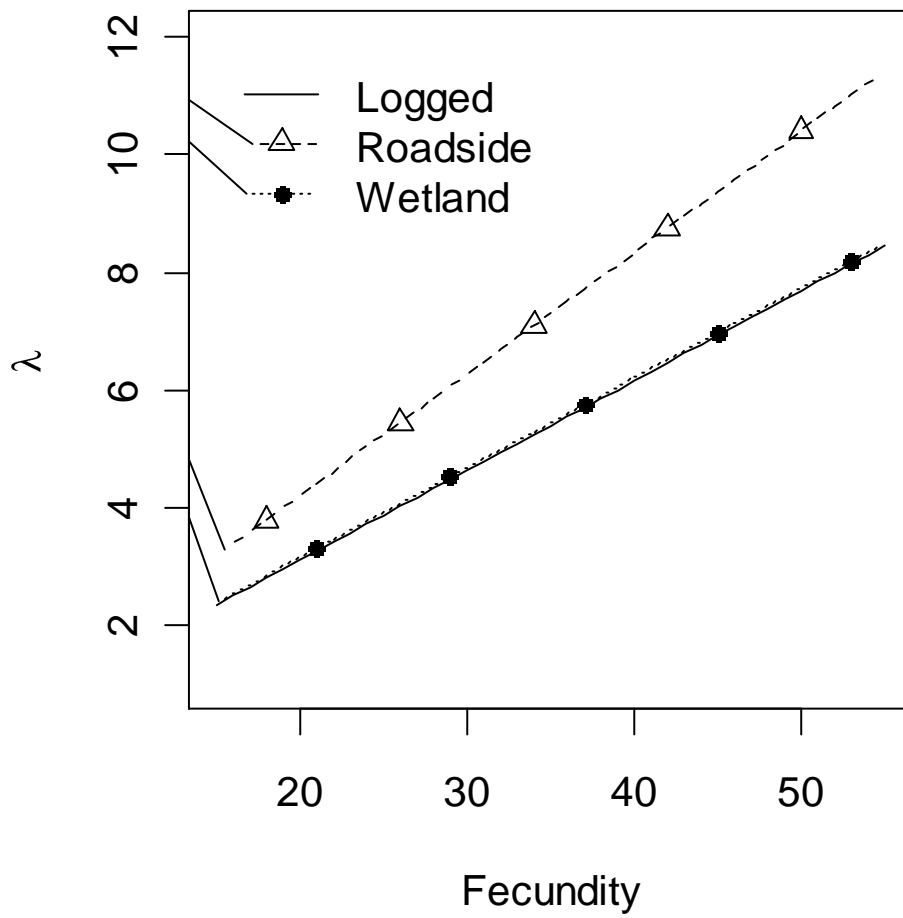


Figure A2. From Chapter 5. Effect of fecundity on population growth rate λ in logged, roadside, and wetland environments.

Species	C	Species	C
<i>Acer pensylvanicum</i>	5	<i>Galium palustre</i>	8
<i>Acer rubrum</i>	1	<i>Galium triflorum</i>	5
<i>Ageratina altissima</i>	3	<i>Gaultheria procumbens</i>	8
<i>Agrostis stolonifera</i>	0	<i>Gaylussacia baccata</i>	8
<i>Alliaria petiolata</i>	0	<i>Geum aleppicum</i>	6
<i>Amphicarpa bracteata</i>	4	<i>Geum canadense</i>	3
<i>Anagallis arvensis</i>	0	<i>Geum virginianum</i>	6
<i>Antennaria</i> sp.	2	<i>Glyceria striata</i>	8
<i>Apocynum cannabinum</i>	2	<i>Gratiola neglecta</i>	3
<i>Berberis thunbergii</i>	0	<i>Hamamelis virginiana</i>	5
<i>Betula lenta</i>	5	<i>Hypericum mutilum</i>	3
<i>Bidens frondosa</i>	2	<i>Hypericum punctatum</i>	2
<i>Boehmeria cylindrica</i>	5	<i>Impatiens capensis</i>	3
<i>Botrychium virginianum</i>	5	<i>Juncus effusus</i>	2
<i>Bromus</i> sp.	0	<i>Juncus</i> sp.	2
<i>Carex crinita</i>	4	<i>Kalmia latifolia</i>	5
<i>Carex</i> sp.	4	<i>Leersia virginiana</i>	3
<i>Carex</i> sp.	4	<i>Lindera benzoin</i>	5
<i>Cerastium vulgatum</i>	0	<i>Linum virginianum</i>	5
<i>Chenopodium</i> sp.	0	<i>Liriodendron tulipifera</i>	5
<i>Circaea quadrisculata</i>	2	<i>Lobelia inflata</i>	1
<i>Cirsium arvense</i>	0	<i>Lycopus americanus</i>	4
<i>Cirsium vulgare</i>	0	<i>Lysimachia ciliata</i>	4
<i>Cornus florida</i>	4	<i>Lysimachia nummularia</i>	0
<i>Coronilla varia</i>	0	<i>Lysimachia quadrifolia</i>	5
<i>Crataegus</i> sp.	4	<i>Malva neglecta</i>	0
<i>Danthonia compressa</i>	4	<i>Medeola virginiana</i>	7
<i>Dennstaedtia punctilobula</i>	2	<i>Medicago lupulina</i>	0
<i>Desmodium</i> sp.	4	<i>Melampyrum lineare</i>	7
<i>Dryopteris</i> sp.	4	<i>Melilotus alba</i>	0
<i>Eleagnus umbellata</i>	0	<i>Microstegium vimineum</i>	0
<i>Eliocharis</i> sp.	2	<i>Mitchella repens</i>	6
<i>Equisetum</i> sp.	1	<i>Muhlenbergia schreberi</i>	1
<i>Erigeron annuus</i>	0	<i>Nasturtium officinale</i>	0
<i>Erigeron philadelphicus</i>	1	<i>Nyssa sylvatica</i>	6
<i>Euthamia graminifolia</i>	3	<i>Onoclea sensibilis</i>	3
<i>Fragaria virginiana</i>	2	<i>Oxalis stricta</i>	0
<i>Fraxinus americana</i>	5	<i>Panicum clandestinum</i>	1
<i>Galium asprellum</i>	7	<i>Panicum</i> sp.	1
<i>Galium lanceolatum</i>	8	<i>Parthenocissus quinquefolia</i>	3

Table A3. List of species encountered in suppression experiment plots, with *C* values used in floristic quality assessment.

C Species

7 *Phegopteris hexagonoptera*
1 *Phytolacca americana*
4 *Pilea pumila*
6 *Pinus strobus*
0 *Plantago lanceolata*
0 *Plantago major*
6 *Platanthera lacera*
1 *Poa* sp.
0 *Polygonum cespitosum*
2 *Polygonum hydropiperoides*
3 *Polygonum sagittatum*
3 *Potentilla canadensis*
6 *Prenanthes* sp.
0 *Prunella vulgaris*
3 *Prunus serotina*
6 *Quercus alba*
7 *Quercus prinus*
6 *Quercus rubra*
0 *Rosa multiflora*
6 *Rubus hispidus*

C Species

0 *Satureja vulgaris*
2 *Scirpus* sp.
2 *Sisyrinchium antustifolium*
2 *Smilax rotundifolia*
2 *Solidago canadensis*
0 *Sonchus arvensis*
6 *Sparganium americanum*
0 *Stellaria vulgatum*
1 *Symphotrichum* sp.
0 *Taraxacum officinale*
5 *Thelypteris noveboracensis*
1 *Toxicodendron radicans*
8 *Tsuga canadensis*
0 *Tussilago farfara*
4 *Ulmus americana*
6 *Uvularia perfoliata*
5 *Vaccinium* sp.
1 *Viola* sp.
6 *Viola* sp. (stemmed)

Table A3 (cont.). List of species encountered in suppression experiment plots, with *C* values used in floristic quality assessment.

Parameter	Environments		
	Logged	Roadside	Wetland
Comparison of methods of MIVI suppression	Chemical significantly better than mechanical in one year	No difference between chemical and mechanical	No difference between chemical and mechanical
Plant species richness response to method of MIVI suppression	No difference between chemical and mechanical	No difference between chemical and mechanical	Tended to be higher in mechanical than chemical
Response of percent of area left unvegetated	No difference between chemical and mechanical	No difference between chemical and mechanical	Significantly higher in chemical than mechanical
Seed bank persistence	Significantly higher than in other environments	Significantly lower than in other environments	Intermediate
Response of model MIVI populations to herbicide every second year	$\lambda < 1$ (decline)	$\lambda < 1$ (decline)	$\lambda < 1$ (decline)
Response of model MIVI populations to herbicide every third yr	$\lambda > 1$ (growth)	$\lambda > 1$ (growth)	$\lambda > 1$ (growth)
Response of model MIVI populations to herbicide 3 consecutive yrs followed by 3 yrs without	$\lambda > 1$ (growth)	$\lambda < 1$ (decline)	Depends on level of suppression of seed production
Response of model MIVI populations to pathogen	$\lambda > 1$ (growth)	$\lambda > 1$ (growth)	$\lambda > 1$ (growth)
Response of model MIVI populations to pathogen plus herbicide every 3rd year	$\lambda < 1$ (decline)	$\lambda < 1$ (decline)	$\lambda > 1$ (growth)

Table A4. Summary of comparisons from Chapters 3-5 of *M. vimineum* populations and non-target plant communities in logged, roadside, and wetland environments.

Andrea Nafziger Nord **Vita**

EDUCATION

- 2005-Present Ph.D. candidate in Ecology, The Pennsylvania State University, University Park, PA
- 1998 M.S. in Ecology. The Pennsylvania State University, University Park, PA
- 1994 B.A. in Biology with minor in Environmental Studies. Goshen College, Goshen, IN

EMPLOYMENT HISTORY

- 2003-Present Graduate Assistant, Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, PA. Research focuses on ecology of invasive *Microstegium vimineum*. Worked with three faculty members to develop and teach a graduate-level course in identification of local flora (2006, 2007, 2010). TA for undergraduate honors course Soils, Societies, and Civilizations (2008); accompanied the class on trip to Jordan.
- 2002-2003 Interim Assistant Professor of Biology at Goshen College. Sole responsibility for general biology class for non-majors: lectures, labs, and supervision of undergraduate teaching assistants. Duties at the college's environmental education center: curated the herbarium, assisted with programs.
- 1999-2002 Environment/Natural Resources extension worker in western Honduras with the Mennonite Central Committee. Worked with rural mountain communities in natural resource management and other environmental issues.
- 1996-1998 Graduate Assistant, School of Forest Resources, The Pennsylvania State University, University Park, PA. Research focused on plant community outcomes following use of municipal biosolids as fertilizer in reclamation of surface coal mines. Dendrology class TA.

PUBLICATIONS

- Nord, A.N.**, D.A. Mortensen, and E.S.J. Rauschert. 2010. Environmental factors influence early population growth of *Microstegium vimineum* (Japanese stiltgrass). *Invasive Plant Science and Management*, 3(1): 17-25.
- Rauschert, E.S.J. and **A.N. Nord**. 2010. Japanese Stiltgrass: An invader on the move. *Ohio Woodland Journal* 17(2): 15-17.
- Rauschert, E.S.J., D.A. Mortensen, O.N. Bjørnstad, **A.N. Nord**, and N. Peskin. 2010. Slow spread of the aggressive invader *Microstegium vimineum* (Japanese stiltgrass). *Biological Invasions*, 12: 563-579.
- Mortensen, D.A., E.S.J. Rauschert, **A.N. Nord**, and B.P. Jones. 2009. Forest roads facilitate spread of invasive plants. *Invasive Plant Science and Management* 2: 191-199.

SELECTED PRESENTATIONS

- Nord, A.N. and D.A. Mortensen. 2010. "Use of limestone gravel on forest roads increases abundance of *Microstegium vimineum* (Japanese stiltgrass)." Ecological Society of America, Pittsburgh, PA.
- Nord, A.N. and D.A. Mortensen. 2008. "The influence of small-scale environmental factors on early stages of *Microstegium vimineum* (Japanese stiltgrass) population growth." Ecological Society of America, Milwaukee, WI.