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Competitive interaction between *Microstegium vimineum* and first-year seedlings of three central hardwoods[1]

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Marshall, J. M., D. S. Buckley, and J. A. Franklin (Department of Forestry, Wildlife and Fisheries, The University of Tennessee, Knoxville, TN 37996). Competitive interaction between *Microstegium vimineum* and first-year seedlings of three central hardwoods. J. Torrey Bot. Soc. 136: 342–349. 2009.—We established an experiment designed to compare effects of *Microstegium vimineum* (Japanese stiltgrass) on seedlings of three native hardwood species to investigate the hypothesis that competitive effects of *M. vimineum* on juvenile trees will vary across different tree species. Growth and survival of *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus rubra* first-year seedlings were compared in plots with and without *M. vimineum* in three planting beds under 50 percent shade. The tree species studied are abundant and of particular interest in the Central Hardwood Region. *A. rubrum* and *L. tulipifera* seedlings experienced reduced growth in several foliar characteristics in the presence of *M. vimineum*. *Q. rubra* did not exhibit any differences in foliar characteristics between plots with and without *M. vimineum*, however there was a reduction in *Q. rubra* stem weight as a result of the presence of *M. vimineum.* The differential responses of *A. rubrum*, *L. tulipifera*, and *Q. rubra* to the presence of *M. vimineum* observed in this study support the hypothesis that effects of this exotic species will vary across tree species. As a result of reductions in the growth of *A. rubrum* and *L. tulipifera*, the presence of *M. vimineum* in forest understories may reduce the rate at which seedlings of these species are recruited into larger size classes.

Key words: competition, invasive species, Japanese stiltgrass, red maple, red oak, regeneration, yellow-poplar.

Native understory plant communities provide necessary facilitation and inhibition for recruitment of canopy and forest-type defining tree seedlings into larger size classes (George and Bazzaz 1999, Beckage and Clark 2003, Kennedy and Sousa 2006). One of several concerns related to invasions of forests by exotic plant species is that future forest composition may be altered through detrimental effects of exotics on growth and recruitment of tree seedlings into larger size classes. By limiting recruitment of native species, several invasive, exotic plant species have imposed community level impacts (Gordon 1998). These changes in composition may be related to mortality induced by exotic species (e.g., Fagan and Peart 2004); however alterations to growth may delay recruitment of young seedlings into larger size classes. *Microstegium vimineum* (Trin.) A.Camus (Japanese stiltgrass; Poaceae) is a C_4 grass introduced to North America from Southeastern Asia (Fairbrothers and Gray 1972, Sur 1985, Osada 1989). It is found throughout the Eastern United States from Florida to Massachusetts and as far west as Texas (Fairbrothers and Gray 1972, Hunt and Zaremba 1992, Natural Resources Conservation Service 2007). *M. vimineum* is able to acclimate to varying levels of available light (Winter et al. 1982, Horton and Neufeld 1998). This physiological plasticity may contribute to the ability of this species to spread into disturbed forests, which it readily invades (Barden 1987, Cheplick 2006, Oswalt and Oswalt 2007, Marshall and Buckley 2008a, b). Potential for this species to adversely affect the regeneration of native hardwood tree species has recently raised concern on the part of managers.

Competitive ability and effects of *Microstegium vimineum* may vary depending on the strategy of a given competitor and the environment. Under full sunlight, *M. vimineum* effectively out-competes two other grasses, *Lolium perenne* ssp. *multiflorum* (Lam.) Husnot, an aggressive exotic annual,

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and *Muhlenbergia mexicana* (L.) Trin., a native lowland C_4 perennial. Under shade, however, the competitive ability of *M. vimineum* did not differ from the other grasses in the experiment (Leicht et al. 2005). It is likely the poor competitive ability of *M. vimineum* in shade is due partly to low growth rates in low light (Williams 1998, Cole and Weltzin 2005, Marshall and Buckley 2008b). Due to innate differences in the reaction of different tree species to various types of competition, it can be hypothesized that competitive effects of *M. vimineum* on juvenile trees will vary across different tree species.

Although the ability of *Microstegium vimineum* to establish and rapidly spread across landscapes is well known (e.g., Barden 1987, Hunt and Zaremba 1992), information on competitive effects of this species on hardwood trees is primarily anecdotal. However, in recent field studies under a range of canopy cover conditions, height growth of *Quercus rubra* L. (northern red oak; Fagaceae) seedlings decreased as *M. vimineum* biomass increased and reductions in woody stem densities occurred as a result of the presence of *M. vimineum* (Oswalt et al. 2004, 2007). Quantifying the competitive effects of *M. vimineum* on native tree seedlings will provide further understanding of its impacts on early growth of three tree species having different life history strategies and characteristics.

The objectives of this study were to 1) quantify the competitive effects of *Microstegium vimineum* on the seedling growth of three native central hardwood species and vice versa, and 2) to test the hypothesis that native hardwood tree seedlings will respond differently to competition with this exotic species.

Materials and Methods. STUDY SITE. A randomized complete block design was utilized with three planting beds acting as blocks. Beds were established at the University of Tennessee Forest Resources Research and Education Center at Oak Ridge, TN (36° 00′ 04″ N, 84° 13′ 30″ W). This site is located in the Appalachian Ridge and Valley Physiographic Region. While the location of the study site was an open field, it is within the Appalachian section of the Central Hardwood forest, which is dominated by the Oak-Hickory forest type (Fralish 2003). Soils are an Armuchee channery silty clay loam (Natural Resources Conservation Service 2006). Mean annual temperature is 15 °C and mean annual precipitation is approximately 1500 mm (National Climatic Data Center 2005).

PLANTING BEDS AND PLOTS. Six planting beds were prepared with the application of glyphosate herbicide on 1 February 2006 and tilled with a tractor-mounted roto-tiller on 1 March 2006. Shade houses were installed over each of three beds, and consisted of 50% shade cloth (Gempler's, Janesville, WI) fastened to PVC frames. Shade cloth extended to the soil surface. Twenty-one plots measuring 60 × 60 cm (3 tree species × 2 treatments with or without *Microstegium vimineum* × 3 replicates + 3 pure *M. vimineum*) were established within each shade house, with a 60 cm buffer separating plots and the shade house edge.

SEED COLLECTION, STRATIFICATION, AND PLANTING. *Microstegium vimineum* seed was collected on 20 October 2005 from several existing populations within 0.5 km of the study site. *M. vimineum* plants were dried at 21 °C for 24 h and seeds were collected from dried material with an aspirator. *Quercus rubra* acorns were collected from a single maternal seed source at the Cherokee National Forest Watauga Northern Red Oak Genetic Resource Area on 8 October 2005. Acorns were immediately graded by size and only 2 cm (± 0.1) diameter acorns were selected for planting to minimize variation in stored reserves. *Liriodendron tulipifera* L. (yellow-poplar; Magnoliaceae) seeds were collected from a seed orchard near Knoxville, TN, in 2004 and stored at 4 °C. *Acer rubrum* L. (red maple, Aceraceae) seeds were purchased from Sheffield's Seed Co., Inc. (Locke, NY) with a collection location in Madison County, TN, in 2005.

Microstegium vimineum, *Liriodendron tulipifera*, and *Quercus rubra* seeds were cold stratified in wet sand at 4 °C for 3 months. *Acer rubrum* seeds were soaked for 24 hours and cold stratified in wet sand at 4 °C for 1 month. *A. rubrum*, *L. tulipifera*, and *Q. rubra* seeds were sown in vermiculite on 1 and 2 March 2006, watered daily, and grown at 24 °C in a greenhouse. All tree seedlings were transplanted to the study site on 7 April 2006 with 108 individuals of each species transplanted in all three shade houses (6 individuals × 2 treatments × 3 replicates × 3 houses). *M. vimineum* seed was sown directly on the field plots on 7 April 2006, but due to low germination rates it was re-sown on 5 May 2006 after the shade houses were erected. At both sowing instances, seeds were applied at a rate of 150 seeds per plot on the soil surface. Densities of *M. vimineum* were thinned on 24 May 2006 to 60 individuals per plot. Plots were weeded on a 2–4 week cycle to minimize the influence of non-target species.

Species treatments were randomly placed within each shade house. Plots with tree seedlings contained only one species of tree. Species treatments for a single tree species were replicated three times within each shade house and consisted of control plots of six trees with no *Microstegium vimineum*, treatment plots of six trees with 60 *M. vimineum*, and zero trees with 60 *M. vimineum*. This density of *M. vimineum* individuals is greater than that of the leading edge of spreading populations (Marshall and Buckley 2008a) but less than that occurring in a dense, well established patch (Williams 1998).

PLANT HARVESTING AND GROWTH MEASURES. All tree seedlings were harvested on 2–4 October 2006 and stored in sealed plastic bags at 4 °C until processed. Harvesting was carried out before tree seedling leaf fall. Tree seedlings were harvested with a sharpshooter shovel, removing ample soil to harvest as much of each root system as possible. Leaf area was measured using a LI-3100 Area Meter (LI-COR Biosystems, Lincoln, NE) for all tree seedlings. Roots were separated from above-ground structures and washed to remove soil. All above- and below-ground structures were dried at 55 °C to a constant weight. Above- and below-ground biomass were measured and specific leaf weight (mg/cm^2), area per leaf (cm^2/leaf), and root: shoot ratio were calculated, where shoot biomass consisted of all above-ground biomass including leaf and stem weights.

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

DATA ANALYSIS. A chi-square test was used to test the likelihood that seedling mortality was independent of treatment. We used *t*-tests to identify differences in tree seedling growth variables between treatments with and controls without *Microstegium vimineum*. The ratios of treatments with *M. vimineum* present to controls with *M. vimineum* absent were calculated for each tree species growth variable and differences between species were tested using analysis of variance (ANOVA). For all ANOVAs, Tukey's HSD was used as a post-hoc test. Simple linear regression was used to test for relationships between *M. vimineum* height and tree seedling height, seed mass and *M. vimineum* biomass, and seed count and *M. vimineum* biomass. All analyses were performed with $\alpha = 0.05$ using SAS computer software (Version 9.1, SAS Institute, Inc., Cary NC).

Results. A total of 6 *Acer rubrum*, 9 *Liriodendron tulipifera*, and 6 *Quercus rubra* seedlings died out of the 108 individuals of each species planted. For each species, mortality was statistically independent of the presence of *Microstegium vimineum*. For *A. rubrum*, there were significant differences between treatment plots with and control plots without *M. vimineum* for seedling leaf weight, shoot weight, root weight, total seedling weight, number of leaves per seedling, leaf area, and stem length reduced in the presence of *M. vimineum* (Table 1). For *L. tulipifera*, there were significant differences between treatments and controls in seedling leaf weight, stem weight, shoot weight, root weight, total seedling weight, number of leaves per seedling, leaf area, and specific leaf weight (Table 2). As with *A. rubrum*, these growth parameters were reduced in plots with *M.*

Table 1. Mean *Acer rubrum* seedling growth variables in treatment plots with *Microstegium vimineum* present and control plots with *M. vimineum* absent. An asterisk (*) signifies a significant difference for one tailed *t*-test with 16 df.

Variable	Treatment		Control			
	Mean	SE	Mean	SE	*t*	*P*
Leaf weight (g)	0.72	0.22	2.48	0.43	−3.60	0.001*
Leaf count	15.51	0.80	34.27	2.62	−6.84	< 0.001*
Leaf area (cm^2)	131.11	39.38	466.92	81.94	−3.69	< 0.001*
Area per leaf (cm^2/leaf)	8.09	2.03	12.94	1.75	−1.81	0.044*
Specific leaf weight (mg/cm^2)	5.40	0.26	5.28	0.11	0.44	0.667
Stem length (cm)	21.19	2.51	35.97	2.51	−2.99	0.004*
Stem weight (g)	0.64	0.28	1.51	0.33	−2.01	0.031*
Shoot weight (g)	1.65	0.79	3.99	0.75	−2.14	0.024*
Root weight (g)	1.12	0.50	2.01	0.33	−1.49	0.079
Root:shoot ratio	0.85	0.06	0.59	0.06	3.06	0.004*

vimineum (Table 2). For *Q. rubra*, there were significant differences only in seedling stem weight and shoot weight, which were reduced in plots with *M. vimineum* (Table 3).

Mean *Microstegium vimineum* above-ground biomass, total seed mass, and seed counts did not differ significantly between the presences and absence of the different tree species (Table 4). Mean height of *M. vimineum* did not differ significantly between the mixtures of tree species ($F_{3,20} = 1.91$, $P = 0.161$). There was, however, a significant positive linear relationship between mean tree height and mean *M. vimineum* height ($R^2 = 0.24$, $F_{1,16} = 5.13$, $P = 0.038$). The mean height for each tree species was less than that of *M. vimineum*. Total seed mass per plot was significantly related to total *M. vimineum* biomass per plot ($R^2 = 0.17$, $F_{1,34} = 6.91$, $P = 0.013$). However, *M. vimineum* seed count per plot was not significantly related to biomass ($R^2 = 0.09$; $F_{1,34} = 3.30$; $P = 0.078$).

Of the ratios between treatment with *Microstegium vimineum* present and control with *M. vimineum* absent for growth variables examined, only leaf weight, leaf count, and leaf area differed significantly between species. A ratio of 1.0 signifies no difference between plots with and without *M. vimineum*, a ratio < 1.0 signifies a reduction in growth in the presence of *M. vimineum*, and a ratio > 1.0 signifies an increase in growth in the presence of *M. vimineum*. *Acer rubrum* had a significantly smaller ratio in leaf weight, leaf count, and leaf area than *Quercus rubra* (Fig. 1). These leaf variables for *A. rubrum* did not differ from those of *Liriodendron tulipifera*. While the ratio of *L. tulipifera* leaf weight ratio was approximately 0.4 smaller than *Q. rubra*, it was not significantly different. All three ratios for the leaf variables of *Q. rubra* were near 1.0, suggesting little change in these variables in the presence of *M. vimineum*.

Table 2. Mean *Liriodendron tulipifera* seedling growth variables in treatment plots with *Microstegium vimineum* present and control plots with *M. vimineum* absent (SE). An asterisk (*) signifies a significant difference for one tailed *t*-test with 16 df.

Variable	Treatment		Control			
	Mean	SE	Mean	SE	*t*	*P*
Leaf weight (g)	3.48	1.00	8.39	2.13	−2.08	0.027*
Leaf count	10.61	1.16	20.24	3.61	−2.54	0.011*
Leaf area (cm^2)	1007.56	270.88	2130.25	574.52	−1.77	0.048*
Area per leaf (cm^2/leaf)	85.28	15.31	93.43	9.73	−0.45	0.330
Specific leaf weight (mg/cm^2)	3.32	0.20	4.07	0.14	−3.13	0.003*
Stem length (cm)	40.83	8.52	46.57	7.43	0.51	0.309
Stem weight (g)	3.74	1.37	7.45	3.10	−1.10	0.144
Shoot weight (g)	7.22	2.33	15.84	5.19	−1.52	0.075
Root weight (g)	2.32	0.67	5.97	1.33	−2.44	0.013*
Root:shoot ratio	0.45	0.06	0.49	0.06	−0.47	0.324

Table 3. Mean *Quercus rubra* seedling growth variables in treatment plots with *Microstegium vimineum* present and control plots with *M. vimineum* absent (SE). An asterisk (*) signifies a significant difference for one tailed *t*-test with 16 df.

Variable	Treatment Mean	Treatment SE	Control Mean	Control SE	*t*	*P*
Leaf weight (g)	1.49	0.15	1.94	0.24	−1.60	0.064
Leaf count	6.14	0.44	6.64	0.49	−0.76	0.229
Leaf area (cm^2)	181.31	22.90	186.64	32.81	−0.13	0.448
Area per leaf (cm^2/leaf)	29.07	2.44	26.51	2.99	0.66	0.742
Specific leaf weight (mg/cm^2)	8.43	0.33	12.36	2.47	−1.58	0.067
Stem length (cm)	20.45	1.42	22.03	0.81	0.97	0.173
Stem weight (g)	0.93	0.08	1.30	0.12	−2.63	0.009*
Shoot weight (g)	2.42	0.21	3.24	0.28	−2.38	0.015*
Root weight (g)	4.32	0.28	4.79	0.41	−0.95	0.179
Root:shoot ratio	1.94	0.10	1.99	0.18	−0.25	0.403

Discussion. For both *Acer rubrum* and *Liriodendron tulipifera*, there was a reduction in leaf biomass in plots with *Microstegium vimineum* compared to plots without *M. vimineum* (Tables 1, 2). However for *A. rubrum*, this change in leaf weight is explained by a reduced leaf count and leaf area but not specific leaf weight, which did not differ between treatments with and without *M. vimineum* (Table 1). This may be an indication of competition for available soil moisture (Evans 1972). In addition to soil moisture, *M. vimineum* may have competed with *A. rubrum* and *L. tulipifera* for available soil nutrients. The reduction in specific leaf weight and leaf count for *L. tulipifera* suggests competition with *M. vimineum* for soil nutrients (Table 3). Changes in available soil nutrients can affect the mean leaf weight per individual plant, with decreases in available nutrients causing decreases in mean leaf weight (Evans 1972). Increased allocation of energy to roots under below-grown competition is well documented, while competitive effects of shoots can have an opposite effect during below-ground competition (Haugland and Tawfik 1999). Reduction of *L. tulipifera* leaf area when grown with Japanese stiltgrass was similar to reductions observed when *L. tulipifera* was grown with *Poa pratensis* L. (Poaceae) (Kolb and Steiner 1990). Also, *Quercus rubra* exhibited reductions in stem growth in competition with *P. pratensis*, although not significant (Kolb and Steiner 1990). In various habitat types, including forests, the turf grass species *P. pratensis* is considered an invasive species (e.g., Brothers and Spingarn 1992, Larson et al. 2001, Choi and Pavlovic 2002). While soil water and nutrient availability are closely linked, this study was not designed to separate these effects.

Due to the lack of significant differences between any species treatments and the controls, apparently none of the species of first-year tree seedlings imposed significant competitive impacts on *Microstegium vimineum*. Native tree species of this size may not impose enough competitive influence to hinder the spread of *M. vimineum*. Clearly, the situation may be very different with larger saplings and mature trees.

The positive relationship between tree stem length and the height of *Microstegium vimi-*

Table 4. Mean *Microstegium vimineum* total above-ground biomass, seed mass, and seed count with hardwood tree seedlings and in the control (1 SE).

	Microstegium vimineum					
	Biomass (g)		Seed mass (g)		Seed count	
Tree Species	Mean	SE	Mean	SE	Mean	SE
Acer rubrum	213.07	27.26	6.26	0.62	10084.52	1829.80
Liriodendron tulipifera	155.79	22.71	5.23	1.05	8102.94	2327.42
Quercus rubra	157.24	19.90	5.14	0.79	8667.04	1916.34
Control	181.97	18.66	6.22	0.89	9819.63	1741.35
F (df = 3,30)	1.53		0.57		0.69	
P	0.22		0.64		0.56	

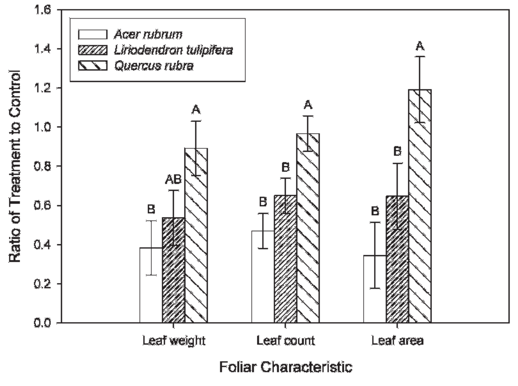

FIG. 1. Ratios for total leaf weight, leaf count and leaf area between treatment plots with *Microstegium vimineum* present and control plots with *M. vimineum* absent for *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus rubra*. Unique letters between species indicate significant differences.

neum above the soil surface is most likely related to the growth habit of *M. vimineum*. The individual grass stem lengths ranging from 60–100 cm (Marshall and Buckley 2008b) result in *M. vimineum* becoming prostrate, lying on the forest floor. In the study plots, the neighboring tree seedlings provided a support structure that allowed *M. vimineum* to extend a canopy higher above the soil surface. By providing structure for *M. vimineum* stems, holding them higher above the soil surface, tree seedlings may be increasing the distance of primary dispersal of *M. vimineum* seeds as they are shed from the parent plant. An increase in stem height has been suggested as an important factor in distance of primary dispersal for various herbaceous plants (Verkaar et al. 1983, Cheplick 1998). A strong linear relationship between *M. vimineum* above-ground biomass and the number of seeds produced has been previously described by Williams (1998). While a significant regression relationship was not indicated in this study, a similar trend was found. The lack of significance may have resulted from the methodology used. Williams (1998) measured biomass and seed production on an individual plant level, instead of on a plant stand level as in this study.

Ratios between treatment and control (presented in Fig. 1) provided standardized values that facilitate comparisons between the different species. Although both *Acer rubrum* and *Liriodendron tulipifera* exhibited significantly smaller ratios than *Quercus rubra* for leaf count and leaf area, the mechanisms differed. *L. tulipifera* reduced leaf area was primarily the result of fewer leaves that were thinner under competition with *Microstegium vimineum*, as illustrated by the reduction in specific leaf weight, although the individual leaves were similar in area. *A. rubrum* showed reductions in both leaf number and the area of individual leaves, but no significant difference in leaf thickness. Water stress is known to reduce leaf size (Evans 1972, Nobel 1980) suggesting that *A. rubrum*, which is found on moist soils and typically has a shallow root system, may have been more affected than the other tree species by root competition.

The competitive influence imposed by *Microstegium vimineum* varies depending on the species it is interacting with, as illustrated by Leicht et al. (2005) and the results from this study. The short-term nature of the study presented here, and that of Leicht et al. (2005), limits extensive application of the results. Unfortunately, the annual and multinodal growth habit of *M. vimineum* complicates maintaining precise numbers of this species per plot in multi-year studies. While mortality of tree seedlings was not related to *M. vimineum* competition, the reduced growth in *Acer rubrum* and *Liriodendron tulipifera* could conceivably have implications for future composition of Central Hardwood forests, particularly if competition with *M. vimineum* persists. Both species are important as dominant and co-dominant canopy trees, which are the defining species for several different forest types (Beckage and Clark 2003, Schmidt and McWilliams 2003). While the density of plants within the treatment plots may explain the reduction in growth, there are still the potential changes in tree seedling growth due to the alteration of the understory plant communities. The addition of *M. vimineum* to the neighboring forest understory drastically changed the understory plant structure and abundance (Marshall 2007). By adding this species to the understory plant community, the competitive interaction between *M. vimineum* and important native hardwood species may limit early growth of tree seedlings. The survivorship of juvenile trees over time, in turn the advanced regeneration of forests, is closely related to soil moisture availability and growth rates (Caspersen and Kobe 2001). While competition is only one aspect of the forest regeneration process (Royo and Carson

2008), reduced growth of seedlings may in turn alter future forest composition and succession by delaying the recruitment of tree seedlings into larger size classes., which exemplifies the need for multi-year studies quantifying the competitive interactions between recurring stands of *M. vimineum* and these native hardwood tree species.

Literature Cited

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

Beckage, B. and J. S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. Ecology 84: 1849–1861.

Brothers, T. S. and A. Spingarn. 1992. Forest fragmentation and alien plant invasions of Central Indiana old-growth forests. Conserv. Biol. 6: 91–100.

Caspersen, J. P. and R. K. Kobe. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. Oikos 92: 160–168.

Cheplick, G. P. 1998. Seed dispersal and seedling establishment in grass populations, p. 84–105. *In:* G. P. Cheplick [ed.], Population Biology of Grasses Cambridge University Press, New York, NY.

Cheplick, G. P. 2006. A modular approach to biomass allocation in an invasive annual (*Microstegium vimineum*; Poaceae). Am. J. Bot. 93: 539–545.

Choi, Y. D. and N. B. Pavlovic. 2002. Experimental restoration of native vegetation in Indiana Dunes National Lakeshore. Restor. Ecol. 6: 118–129.

Cole, P. G. and J. F. Weltzin. 2005. Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. Biol. Invasions 7: 477–488.

Evans, G. C. 1972. The Quantitative Analysis of Plant Growth University of California Press, Berkeley, CA. 734 p.

Fagan, M. E. and D. R. Peart. 2004. Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. For. Ecol. Manage. 194: 95–107.

Fairbrothers, D. E. and J. R. Gray. 1972. *Microstegium vimineum* (Trin.) A.Camus (Gramineae) in the United States. Bull. Torrey Bot. Club 99: 97–100.

Fralish, J. S. 2003. The Central Hardwood forest: Its boundaries and physiographic provinces, p. 1–20. *In:* J. W. Van Sambeek, J. O. Dawson, F. Ponder Jr., E. F. Loewenstein, and J. S. Fralish [eds.], Proceedings of the 13th Central Hardwood Forest Conference, Gen. Tech. Rep. NC-234. United States Department of Agriculture Forest Service, North Central Research Station, St Paul, MN.

George, L. O. and F. A. Bazzaz. 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology 80: 833–845.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecol. Appl. 8: 975–989.

Haugland, E. and M. Tawfiq. 1999. Root and shoot competition between established grass species and newly sown seedlings during spring growth. Grass Forage Sci. 56: 193–199.

Horton, J. L. and H. S. Neufeld. 1998. Photosynthetic responses of *Microstegium vimineum* (Trin.) A.Camus, a shade-tolerant, C4 grass, to variable light environments. Oecologia 114: 11–19.

Hunt, D. M. and R. E. Zaremba. 1992. The northeastward spread of *Microstegium vimineum* (Poaceae) into New York and adjacent states. Rhodora 94: 167–170.

Kennedy, P. G. and W. P. Sousa. 2006. Forest encroachment into a Californian grassland: examining the simultaneous effects of facilitation and competition on tree seedling recruitment. Oecologia 148: 464–474.

Kolb, T. E. and K. C. Steiner. 1990. Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: effects of shading and grass root competition. For. Sci. 36: 34–44.

Larson, D. L., P. J. Anderson, and W. Newton. 2001. Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. Ecol. Appl. 11: 128–141.

Leicht, S. A., J. A. Silander Jr., and K. Greenwood. 2005. Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A.Camus. J. Torrey Bot. Soc. 132: 573–580.

Marshall, J. M. 2007. Establishment, Growth, Spread, and Ecological Impacts of *Microstegium vimineum* in Central Hardwood Forests. Ph.D. dissertation. Univ. of Tennessee, Knoxville, TN.

Marshall, J. M. and D. S. Buckley. 2008a. Influence of litter removal and mineral soil disturbance on the spread of an invasive grass in a Central Hardwood forest. Biol. Invasions 10: 531–538.

Marshall, J. M. and D. S. Buckley. 2008b. Effects of microsites created by selective harvesting on growth of *Microstegium vimineum* in a Central Hardwood forest. For. Sci. 54: 534–542.

National Climatic Data Center. 2005. Local Climatological Data. Retrieved April 27, 2007 from National Oceanic and Atmospheric Administration, Asheville, NC. <http://www.ncdc.noaa.gov/oa/ncdc.html>

Nobel, P. S. 1980. Leaf anatomy and water use efficiency, p. 43–55. *In:* N. C. Turner and P. J. Kramer [eds.], Adaptation of Plants to Water and High Temperature Stress. Wiley, New York, NY.

Osada, T. 1989. Illustrated Grasses of Japan. Heibonsha Ltd. Publishers, Tokyo.

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, p. 1–9. *In:* D. A. Yaussy, D. M. Hix, R. P. Long, and P. C. Goebel [eds.], Proceedings of the

14th Central Hardwood Forest Conference, Gen. Tech. Rep. NE-316. United States Department of Agriculture Forest Service, Northeastern Research Station, Newton Square, PA.

OSWALT, C. M. AND S. N. OSWALT. 2007. Winter litter disturbance facilitates the spread of the nonnative invasive grass *Microstegium vimineum* (Trin.) A.Camus. For. Ecol. Manage. 249: 199–203.

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. For. Ecol. Manage. 242: 727–732.

ROYO, A. A. AND W. P. CARSON. 2008. Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. Can. J. For. Res. 38: 1634–1645.

SCHMIDT, T. L. AND W. H. MCWILLIAMS. 2003. Shifts and future trends in the forest resources of the Central Hardwood region, p. 21–31. *In:* J. W. Van Sambeek, J. O. Dawson, F. Ponder Jr., E. F. Loewenstein, and J. S. Fralish [eds.], Proceedings of the 13th Central Hardwood Forest Conference, Gen. Tech. Rep. NC-234. United States Department of Agriculture Forest Service, North Central Research Station, St Paul, MN.

SUR, P. R. 1985. A revision of the genus *Microstegium* Nees (Poaceae) in India. J. Econ. Taxon. Bot. 6: 167–176.

NATURAL RESOURCES CONSERVATION SERVICE. 2006. Web Soil Survey. Retrieved May 19, 2007 from United States Department of Agriculture. <http://websoilsurvey.nrcs.usda.gov/>

NATURAL RESOURCES CONSERVATION SERVICE. 2007. The PLANTS Database. Retrieved April 27, 2007 from United States Department of Agriculture, Baton Rouge, LA. <http://plants.usda.gov>

VERKAAR, H. J., A. J. SCHENKEVELD, AND M. P. VAN DE KLASHORST. 1983. The ecology of short-lived forbs in chalk grasslands: dispersal of seeds. New Phytol. 95: 335–344.

WILLIAMS, L. D. 1998. Factors Affecting Growth and Reproduction in the Invasive Grass *Microstegium vimineum*. M.S. thesis. Appalachian State Univ., Boone, NC.

WINTER, K., M. R. SCHMITT, AND G. E. EDWARDS. 1982. *Microstegium vimineum*, a shade adapted C-4 grass. Plant Sci. Lett. 24: 311–318.