Biol Invasions (2010) 12:2069–2080
DOI 10.1007/s10530-009-9609-y

ORIGINAL PAPER

Establishment of an invasive grass in closed-canopy deciduous forests across local and regional environmental gradients

Cynthia D. Huebner

Received: 20 March 2009 / Accepted: 6 October 2009 / Published online: 20 October 2009

Abstract Establishment of *Microstegium vimineum*, an invasive exotic grass, in closed-canopy U.S. eastern forests was evaluated across a local (roadside to forest interior) and regional (across two geographic provinces) environmental gradient in West Virginia. The two geographic provinces were the Allegheny Plateau (more mesic) and the Ridge and Valley Province (more xeric). Biotic, abiotic, and disturbance variables were measured in (1) systematically located plots, starting from the roadside and extending 50 m into the forests, and (2) randomly selected, forest interior plots, with equal numbers of plots containing or not containing *M. vimineum*. Associations between the variables and the presence of *M. vimineum* at both scales were evaluated using generalized linear models. Relative importance of the variables related to *M. vimineum* establishment in the forest interior plots at the regional scale was determined using logistic regression. Results confirmed *Microstegium vimineum*'s reduced reproductive capacity in the forest interior compared to the roadside. Patches of *M. vimineum* in the forest interiors across the regional gradient were best defined by high native plant richness and diversity. Greater canopy opening, more moss, and shallower litter depths were also positively and significantly associated with *M. vimineum* presence, but only during the driest sample year.

Keywords Environmental gradient · Forest interiors · Invasive plants · *Microstegium vimineum*

Abbreviations

AIC	Akaike information criterion
CL	Confidence limits
CWD	Coarse woody debris
H–S–V	Herb/shrub/vine
MNF	Monongahela National Forest
NA	Not applicable
PAR	Photosynthetically active radiation
R–V	Ridge and Valley Province
T-S	Tree seedling

Introduction

Undisturbed, closed-canopy forests are considered less susceptible to invasion than other more open habitats. However, a recent estimate showing that 40% of all global invasive exotic plant species and 52% of all North American invasive exotic plant species are shade tolerant suggests that forests are indeed vulnerable to invasion (Martin et al. 2009). Early establishment of invasive plant populations, assuming a seed source exists, is driven by environmental factors, including available resources

C. D. Huebner (✉)
Northern Research Station, USDA Forest Service,
180 Canfield Street, Morgantown, WV 26505, USA
e-mail: chuebner@fs.fed.us; cindy.huebner@gmail.com

(Radosevich et al. 2003; Theoharides and Dukes 2007). Some of these changes in resources of seemingly undisturbed forests may be caused by small-scale disturbances on the forest floor, i.e., animal foraging (Brown 2000), or in the canopy, i.e., small gaps due to tree limb loss or sapling mortality. Nonetheless, forest floors are patchy in terms of nutrients (Fitter et al. 2000) and light (i.e., sunflecks; Chazdon and Pearcy 1991), without any apparent causal disturbance agent. Site invasibility also has been both positively (Lonsdale 1999; Stohlgren et al. 1999; Gilbert and Lechowicz 2005; Huebner and Tobin 2006) and negatively (Tilman 1997; Kennedy et al. 2002) related to native species richness and productivity. Discrepancies between these findings, especially those conducted at a fine scale, may be a function of habitat type and environmental stress (Richardson et al. 1994; Pyšek et al. 2002).

Plant response to environmental gradients has been a definitive force behind plant species composition and diversity (Urban et al. 2000; Pausas and Austin 2001) as well as a plausible explanation for both species displacement via competition for resources (Pickett and Bazzaz 1976) and coexistence via resource partitioning among species (Silvertown 2004). The goal of this research is to observationally evaluate an invasive plant species, in this case *Microstegium vimineum* (Japanese stiltgrass, Nepalese browntop), across environmental gradients in search of resource limitation patterns. Such patterns may include where along these gradients *M. vimineum* is most likely to be displaced by, coexist with, or out-compete native plant species subjected to the same environmental conditions.

U.S. eastern forests with understories saturated with *M. vimineum* have been attributed to prior tree canopy disturbances including hemlock woolly adelgid (Orwig and Foster 1998; Eschtruth et al. 2006), ice storms (pers. obs.), timber harvests (Oswalt et al. 2007; Marshall and Buckley 2008a), a lack of deer herbivory compared to associated native species (Griggs et al. 2006; Baiser et al. 2008; Eschtruth and Battles 2008), and roads (Cole and Weltzin 2004). Fire has been shown to potentially promote invasion of this species (Glasgow and Matlack 2007). Smaller-scale disturbances such as patchy litter removal have also been shown to promote invasion of this grass (Oswalt and Oswalt 2007; Marshall and Buckley 2008b). However, disturbance does not appear to be necessary for *M. vimineum* establishment in closed-canopy forests (Huebner 2007).

There are documented environmental limitations to *M. vimineum*'s success. This grass is most productive in mesic environments (Barden 1987; Redman 1995) and, despite being a C_4 plant, is drought intolerant (Barden 1987; Webster et al. 2008). While *M. vimineum* is shade-tolerant (i.e., low dark respiration rates and low light compensation points; Winter et al. 1982; Horton and Neufeld 1998), photosynthetically active radiation (PAR) values less than 5–18% of full sunlight appear to reduce *M. vimineum* growth and reproduction significantly (Claridge and Franklin 2002; Cole and Weltzin 2004, 2005; Cheplick 2005). The latter indicates that closed canopy forests, which typically have PAR values of 2–5%, should be less susceptible to invasion by *M. vimineum*.

This research addresses the following question: What abiotic and biotic factors influence establishment success of *M. vimineum* in undisturbed, closed canopy forests across a local (roadside to forest interior) and regional (two geographic provinces) environmental gradient?

Methods

Study species

Microstegium vimineum (Trin.) A. Camus (Integrated Taxonomic Information System; Gleason and Cronquist 1993) is an annual, Asiatic grass that was accidentally introduced to the U.S. (Knoxville, Tennessee) in 1919 (Fairbrothers and Grayt 1972) and first documented in West Virginia in 1956 (Huebner 2003). It is currently listed as a noxious weed in Alabama, Connecticut, Massachusetts (USDA plants.gov), and West Virginia (West Virginia Department of Agriculture). This species is included on at least 11 Northeastern, MidAtlantic, Southeastern, and Midwestern state invasive plant lists within the U.S. *Microstegium vimineum* has also been documented in both Puerto Rico (Global Invasive Species Database 2008) and Turkey (Scholz and Byfield 2000). Invasive characteristics of *M. vimineum* include (1) prolific seed production (Gibson et al. 2002) from both chasmogamous (open) and cleistogamous (closed) flower types (Tanaka 1975), (2) the ability to grow horizontally by rooting at the nodes (Fairbrothers and Grayt 1972), (3) shade tolerance (Winter et al. 1982), (4) a seed bank of at least 3 years (Barden 1987), and (5) an apparent lack of pathogens and herbivores (Baiser et al. 2008; Webster et al. 2008; but see Bradford et al. 2009). Negative impacts attributed to *M. vimineum* on native systems include changing soil chemistry by increasing pH, mineralization, nitrification (Kourtev et al. 1999; Ehrenfeld et al. 2001), and phosphorus availability (McGrath and Binckley 2009*)*. Presence of *M. vimineum* and its thatch have also been attributed to a decrease in soil microarthropod diversity (McGrath and Binckley 2009) and tick abundance (Civitello et al. 2008) both of which could have cascading effects on other trophic levels. Abundant cover of *M. vimineum* has been associated with lower native plant diversity (Oswalt et al. 2007).

Study area

Sixteen sites within West Virginia were selected based on the presence of a contiguous roadside population of *M. vimineum* adjacent to a closed-canopy deciduous forest of approximately 70 or more years of age. The sites were located in three regions: 1) five in the Fernow Experimental Forest (38° 53′ N, 79° 17′ W), Cheat-Potomac Ranger District of the Monongahela National Forest (MNF) in the Allegheny Plateau (Fernow), 2) six in Cooper's Rock State Forest and the West Virginia University Forest (39° 39′ N, 79° 47′ W) also in the Allegheny Plateau (Cooper), and 3) five in the Seneca Rocks area (39° 2′ N, 79° 42′ W) of the Cheat-Potomac Range District of the MNF in the Ridge and Valley Province (R–V: Fig. 1).

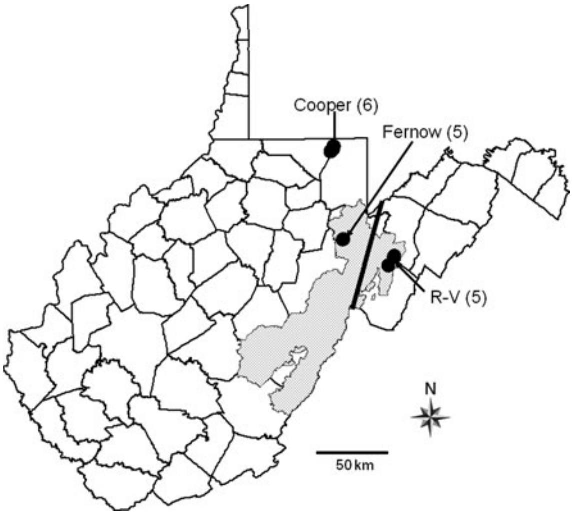

Fig. 1 General site locations across a regional environmental gradient in West Virginia, USA. County borders are included and the line roughly divides the Allegheny Plateau (to the West) and the Ridge and Valley (R–V) Province (to the East). Fernow (5 sites, Tucker county) = Fernow Experimental Forest, Cheat-Potomac Ranger District of the MNF in the Allegheny Plateau, Cooper (6 sites, Preston county) = Cooper State Forest and the West Virginia University Forest in the Allegheny Plateau, and R–V (5 sites, Pendleton and Grant counties) = Seneca Rocks and Smoke Hole area of the Cheat-Potomac Ranger District of the MNF in the R–V Province

The Fernow, Cooper, and R–V sites range in elevation between 585–707 m, 664–720 m, and 592–903 m, respectively. Annual precipitation averages approximately 160 cm for both the Fernow and Cooper sites, while it is about 79 cm annually for the R–V sites (Clarkson 1964). The highest average annual temperature is approximately 23–25°C for the Fernow and Cooper sites, but 30°C for the R–V sites (NOAA, National Climatic Data Center website). The Fernow and Cooper sites are mixed mesophytic forests and the R–V sites are oak-dominated forests. Thus, the Fernow and Cooper sites are more similar in terms of topography and plant species composition. Despite these similarities, the Cooper sites tend to have a less species-rich understory than the Fernow sites. Estimated time of *M. vimineum* arrival for the Fernow and Cooper sites is 2003. *Microstegium vimineum* was estimated to have arrived in the R–V sites in 1996 after extensive flooding of the South Branch of the Potomac River and its tributaries. Slope aspect and inclination of each of the sites in the three regions varied such that uphill/downhill slopes and south-west vs. north-east slopes were represented in each of three areas. Most of the roadside *M. vimineum* populations were 1–5 m wide and at least 20 m long along the roads. However, two of the Cooper sites were adjacent to an area with a larger swath (about 12 m wide) of *M. vimineum* mixed with other species. While most of the roads were limestone gravel, five were paved.

Sampling design

Each site was composed of a 10 m transect parallel to the road and situated within a contiguous roadside *M. vimineum* population that was at least 20 m long.

From this roadside transect, 9 perpendicular transects, each 1.25 m apart, were extended 50 m into the adjacent forest. The two edge transects and a central transect 5 m from either edge (hereafter referred to as the systematic transects) were used to systematically place 1-m^2 plots (0.625 m radius; i.e., the actual circular area of each plot was just over 1 m^2 or 1.2 m^2). Along each of the three systematic transects, the first 1-m^2 plot (0 m) was placed at the roadside just outside the forest canopy edge while subsequent plots fell under the forest canopy and were located every 5 m until 20 m was reached, and then every 10 m until 50 m was reached. If *M. vimineum* was present along any of the nine possible transects at the 5 m plot and beyond, a non-overlapping 1-m^2 plot was established and sampled (Fig. 2).

Sites were sampled in late August in 2005, 2006, and 2007 in order to estimate the cover of *M. vimineum* when it has attained its full size before senescence. Within each 1-m^2 plot, percent cover of all species (including tree seedlings under 1 m, shrubs, vines, and herbaceous plants), moss, bare ground, coarse woody debris, and rock was determined. Above each 1-m^2 plot, instantaneous light (Quantum meter, Spectrum Technologies) and a spherical densiometer (Lemmon Forest Densiometers) reading (percent canopy opening) were measured. Cover, stem counts (2006 and 2007 only), stem height (2005 and 2006 only) of the tallest stem in each 1-m^2 plot, and inflorescence type count (2005 and 2006 only; chasmogamous or cleistogamous) of the tallest stem of *M. vimineum* were also determined. Plot set up and sampling started at the 50 m point and ended at the roadside to prevent the potential of spreading *M. vimineum* seed; shoes were checked for soil and seed. Just outside each of the systematically located 1-m^2 plots, a 15 × 15 cm and 10 cm deep soil sample was taken in late August for determination of soil total C and N (Fig. 2). After collecting each soil sample, the area was re-covered carefully with the litter removed before taking the soil. The total C and N percentages were determined by the University of Maine Analytical Lab.

Data analysis

Using only the 24 plots on the three systematic transects that were sampled whether or not *M. vimineum* was present, *M. vimineum* cover, stem height, chasmogamous and cleistogamous inflorescence counts and select biotic and abiotic environmental variables were compared across sites (combined distances, regional gradient) and distances (combined

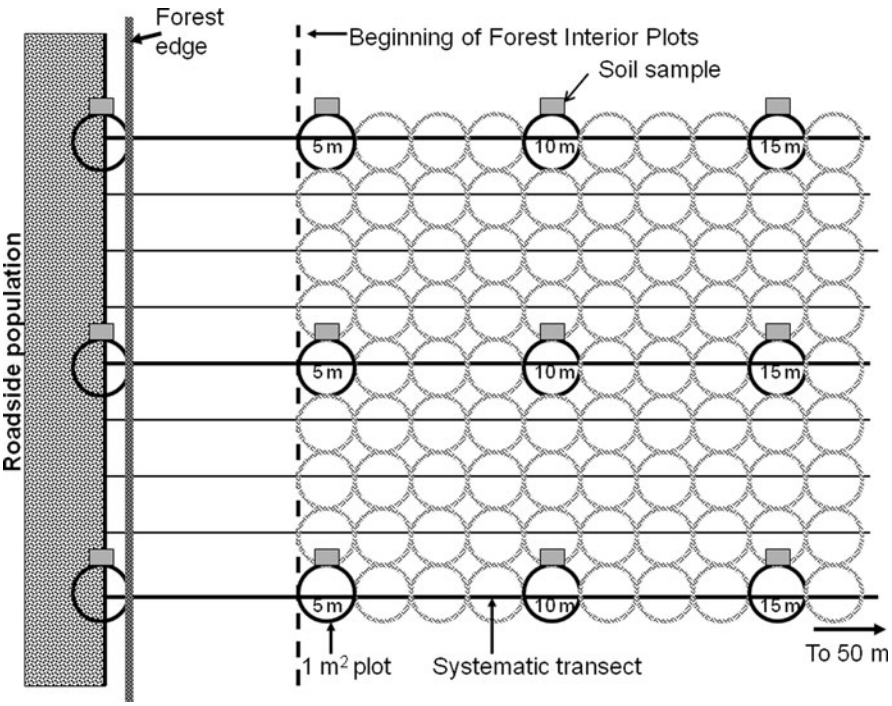

Fig. 2 Sampling design. Dark circles represent the systematically sampled 1-m^2 plots, while the gray circles represent potential plot locations if *M. vimineum* was found to be present in the forest interior. Only 1-m^2 plots through 16 m for each 50 m transect are shown

sites, local gradient) using a separate generalized linear model for each of the 3 years. Each year was analyzed separately because the sample size did not allow for an additional covariate of time and existence of possible temporal trends would be useful to document. The measured biotic variables included herb/shrub/vine and tree seedling species richness and diversity. Diversity was calculated using Shannon's index (Begon et al. 1996). Light (μmol m^{-2} s^{-1}), canopy opening (%), moss (%), bare ground (%), total soil N and C (%, in 2005 only), coarse woody debris (%), and litter depth (cm) were the abiotic variables. A gamma distribution (skewed distribution) with a log link function (nonlinear transformation of the predicted values) was used for all variables except herb/shrub/vine and tree seedling diversity, which were normally distributed, and herb/shrub/vine and tree seedling richness, which were represented by a negative binomial distribution (count data and skewed distribution) and a log link function. Herb/shrub/vine richness and diversity values included *M. vimineum*, if present, for this general comparison among site types and within each site type. All variables, including site, were considered fixed effects.

Based on the measured light levels and densiometer estimates, forest interior plots were conservatively defined as all plots 5 m and beyond the roadside population. Cover (all 3 years) and stem counts (2006 and 2007 only) in plots containing *M. vimineum* in the forest interior were compared across sites for each year using a generalized linear model procedure (Proc GenMod, SAS v. 9.1). Cover was evaluated using a gamma distribution with a log link function and stem counts were evaluated using a negative binomial distribution with a log link function.

Because there were always more plots without *M. vimineum* than with *M. vimineum*, a random selection from all plots without *M. vimineum* equal to the number of plots with *M. vimineum* was made for each year. Using this new set of data for each site containing equal numbers of *M. vimineum* plots and plots without *M. vimineum*, all variables were first analyzed with a generalized linear model procedure (Proc GenMod, SAS v. 9.1). All variables except seedling and herb/shrub/vine diversity and richness were modeled using a gamma distribution with a log link function. The richness variables were modeled using a negative binomial distribution with a log link function and the diversity variables were modeled using a normal distribution (Proc GenMod, SAS v. 9.1). *Microstegium vimineum* counts and cover were removed from the data prior to calculating richness and diversity when comparing plots containing or not containing *M. vimineum*. The generalized linear model analysis were used to reduce the number of variables to those that significantly influenced *M. vimineum* establishment; variables that were significant (using $P < 0.1$, as a first-stage separation of potentially important variables) determinants of *M. vimineum* presence were included in a logistic regression analysis with backwards selection ($P < 0.05$; Proc Logistic, SAS v. 9.1) for each site type and year. The logistic regression analysis determined which of the known important variables had the most relative influence on *M. vimineum* establishment in forest interiors. Richness and diversity variables were run in separate equations due to multicollinearity (Pearson $r > 0.5$). Each of the 3 years was analyzed separately because (1) sample size changed as new plots were colonized by *M. vimineum*, meaning the analyses may not be truly a repeated measure (nor are they completely unbiased), (2) the sample size did not allow for an additional covariate of time, and (3) documentation of temporal trends provided additional information that could be compared with the local gradient variables described earlier.

Results

Local gradient

Cover ($\chi^2_{2005} = 68.72$, $P_{2005} < 0.0001$; data for 2006 and 2007 had similar values for all variables, unless stated otherwise), stem height ($\chi^2_{2005} = 56.43$, $P_{2005} < 0.0001$, $N = 48$), and cleistogamous inflorescences ($\chi^2_{2005} = 14.35$, $P_{2005} = 0.006$, $N = 48$) of *M. vimineum* were significantly greater in the roadside plots (0 m) compared to the forest interior plots for all years measured (stem height and inflorescence information was only measured in 2005 and 2006). There were no significant distance differences for chasmogamous inflorescences in 2005 ($P = 0.61$, $N = 48$), though it shared a similar trend with 2006 in which there were significantly more chasmogamous inflorescences ($\chi^2_{2006} = 3.93$, $P_{2006} = 0.047$, $N = 48$) at

0 m than the forest interior plots. Herb/shrub/vine richness ($\chi^2_{2005} = 78.12$, $P_{2005} = < 0.0001$, $N = 48$) and diversity ($\chi^2_{2005} = 55.53, P_{2005} < 0.0001, N = 48$) were significantly higher at 0 m compared with the interior plots. Tree seedling richness ($\chi^2_{2005} =$ 31.02.96, $P_{2005} < 0.0001$, $N = 48$) and diversity ($\chi^2_{2005} = 20.36, P_{2005} = 0.0048, N = 48$) were significantly lower at 0 m compared with the interior plots. While roadside plots differed significantly with interior plots, there were not significant differences in *M. vimimeum* plant measures or species richness or diversity measures when comparing distances 5 m or more into the forest interior.

The roadside plots (0 m) had significantly greater canopy opening ($\chi^2_{2005} = 162.48$, $P_{2005} < 0.0001$, $N = 48$) and higher light values ($\chi^2_{2005} = 191.48$, $P_{2005} < 0.0001, N = 48$) than all interior plots for all 3 years. All interior light values were less than 70 µmol m^{-2} s^{-1} and most were less than 30 µmol m^{-2} s^{-1}. Similarly, coarse woody debris ($\chi^2_{2005} =$ 23.02, $P_{2005} = 0.0017$, $N = 48$), total C ($\chi^2_{2005} =$ 50.34, $P_{2005} < 0.0001$, $N = 48$), and total N ($\chi^2_{2005} = 61.51$, $P_{2005} < 0.0001 < N = 48$) all were significantly lower at 0 m compared to all interior plots. In contrast, moss cover tended to be more abundant at 5 m and 10 m, showing a significant effect in all years ($\chi^2_{2005} = 20.82$, $P_{2005} = 0.0040$, $N = 48$). Bare ground cover was significantly greater at 0 m than interior plots in all years ($\chi^2_{2005} = 41.37$, $P_{2005} < 0.0001$, $N = 48$). Litter depth and rock showed no apparent pattern with increasing distance from the road. Aside from moss cover, the patterns (or lack of) for the biotic and abiotic variables support separating roadside and forest interior plots at the 5 m distance. Means and standard errors for each variable at each distance are available upon request, but are not presented here.

Regional gradient

Analysis of forest interior plots (averaged within each site) that contained *M. vimineum* showed no significant difference in percent cover ($P_{2007} = 0.15$, $N = 14$) or stem count ($P_{2007} = 0.81$, $N = 14$) among the three sites for any of the 3 years (only 2007 data, which had the largest number of *M. vimineum* containing plots, are presented here). Percent cover per 1-m^2 forest interior plot containing *M. vimineum* averaged between 0.77 and 1.84, while stem counts per 1-m^2 plot averaged between 10.9 and 14.2 across the three sites in 2007.

Using all forest interior plots, there were no significant differences in cover or stem height among the three site types (i.e., along the regional environmental gradient) in any year ($P_{2005} = 0.79$, $P_{2005} = 0.90$, respectively), but the R–V sites did tend to have shorter *M. vimineum* stems than both the Fernow and Cooper sites in 2006. Cleistogamous inflorescences differed significantly among sites in 2005 ($\chi^2_{2005} = 6.96$, $P = 0.03$), but not in 2006 ($P = 0.94$). There were no significant site differences in either year ($P_{2005} = 0.90$; $P_{2006} = 0.30$) for chasmogamous inflorescences, though they appeared to decrease in number between 2005 and 2006, especially in the Cooper and R–V sites. The Fernow sites were significantly more rich ($\chi^2_{2005} = 21.98$, $P < 0.0001$) and diverse ($\chi^2_{2005} = 22.97, P < 0.0001$) in herb-shrub-vine species than both the Cooper and R–V sites in all 3 years. Tree seedling richness ($P = 0.80$) and diversity ($P = 0.92$) did not differ significantly among the sites for any of the 3 years. Total soil C ($P = 0.49$) and N ($P = 0.58$) and coarse woody debris ($P = 0.42$) did not differ significantly among the sites for all years measured. Moss cover ($P = 0.06$) in the R–V sites was marginally significantly less than moss cover in the Fernow sites in both 2006 and 2007 and showed a similar trend in 2005. Rock cover was significantly greater in the R–V and Fernow sites than the Cooper sites for all years ($\chi^2_{2005} = 7.32$, $P_{2005} = 0.03$). The Cooper sites had significantly shallower litter depths ($\chi^2_{2005} = 7.20$, $P_{2005} = 0.03$) than both the Fernow and R–V sites in 2005 but not 2006 or 2007. There was a trend for bare ground to increase and litter depth to decrease over time. Amount of light did not vary significantly among the sites over the 3 years. Though canopy opening ($\chi^2_{2005} = 23.35$, $P < 0.0001$) differed significantly among the sites for all 3 years, the pattern varied. However, there was a trend for the Cooper sites to have more open canopies than the Fernow and R–V sites in 2006 and 2007 (Table 1).

A comparison of forest interior plots with and without *M. vimineum* in 2005 showed that herb/shrub/vine diversity ($\chi^2 = 4.68$, $P = 0.031$), tree seedling richness ($\chi^2 = 5.07$, $P = 0.024$) and diversity ($\chi^2 =$ 3.26, $P = 0.071$), coarse woody debris ($\chi^2 = 5.97$, $P = 0.015$), and total soil C ($\chi^2 = 3.37$, $P = 0.066$) cover were all significant at $P < 0.1$ in separate

Table 1 Comparison of *M. vimineum* growth, biotic, and abiotic variables across a regional gradient using the systematic plots

Variable	Year	Regional gradient (most mesic to most xeric)		
		Fernow $N = 5$	Cooper $N = 6$	R–V $N = 5$
Cover (%)	2005	6.11 (1.87)	7.49 (1.86)	6.88 (1.97)
	2006	5.49 (1.79)	7.92 (1.96)	6.96 (1.81)
	2007	6.09 (1.93)	5.06 (1.48)	4.75 (1.50)
Stem height (cm)	2005	9.85 (2.51)	9.41 (2.05)	10.47 (2.31)
	2006	8.55 (2.11)	7.73 (1.74)	5.68 (1.48)
Cleistogamous	2005	1.41 (0.41)a	1.34 (0.36)a	0.90 (0.24)b
Inflorescences/stem	2006	1.03 (0.24)	1.02 (0.25)	1.09 (0.29)
Chasmogamous	2005	0.09 (0.03)	0.09 (0.04)	0.13 (0.04)
Inflorescences/stem	2006	0.08 (0.03)	0.01 (0.01)	0.05 (0.02)
Herb/shrub/vine richness	2005	7.83 (0.44)a	4.08 (0.25)b	2.25 (0.27)c
Tree seedling richness	2005	2.01 (0.13)	2.05 (0.09)	1.86 (0.12)
Light (μmol m^{-2} s^{-1})	2005	23.10 (2.39)	57.09 (13.24)	47.53 (18.76)
Canopy opening (%)	2005	11.30 (0.60)a	7.64 (0.46)b	7.13 (0.53)b
	2006	5.84 (0.50)ac	6.82 (0.60)a	4.74 (0.49)c
	2007	6.88 (0.43)a	9.20 (0.57)b	7.00 (0.39)a
Coarse woody debris (%)	2005	3.67 (0.43)	4.83 (0.75)	3.79 (0.49)
Total N (%)	2005	0.56 (0.04)	0.73 (0.04)	0.57 (0.03)
Total C (%)	2005	8.96 (0.89)	13.33 (0.74)	10.21 (0.71)
Rock (%)	2005	1.37 (0.42)a	0.40 (0.10)b	2.74 (0.49)a
Moss (%)	2005	1.75 (0.25)	1.31 (0.19)	1.30 (0.24)
	2006	3.04 (0.51)a*	2.34 (0.41)a*	1.04 (0.19)b*
	2007	3.45 (0.60)a*	2.15 (0.37)ac*	1.29 (0.20)c*
Bare ground (%)	2005	0.75 (0.18)	0.88 (0.40)	0.76 (0.23)
	2006	0.64 (0.22)	0.98 (0.50)	0.97 (0.20)
	2007	0.89 (0.36)	1.09 (0.50)	2.99 (1.14)
Litter depth (cm)	2005	2.60 (0.15)a	2.18 (0.09)b	2.82 (0.24)a
	2006	2.52 (0.22)	2.09 (0.12)	2.69 (0.26)
	2007	1.81 (0.13)	2.07 (0.14)	2.01 (0.14)

Values are means of each variable per 1-m^2 plot. Comparisons were analyzed using a generalized linear model; numbers in parentheses are the standard error, and sites with different letters are significantly different ($P < 0.05$). Only 2005 data are shown except where temporal trends differ. Herb/shrub/vine and tree seedling diversity are not shown because the trends are similar to the richness values. Values marked with an * are marginally significantly different with $P = 0.06$)

generalized linear models. Plots with higher herb/shrub/vine diversity, lower seedling richness or diversity, less coarse woody debris, and more total soil C were more likely to contain *M. vimineum*. The logistic regression models using these variables together revealed that none were significant for the Fernow sites, while herb/shrub/vine diversity was significant for the Cooper sites, and both herb/shrub/vine diversity and tree seedling richness were significant variables for the R–V sites. Thus, in 2005, plots with a 0.1 unit increase in herb/shrub/vine diversity at the Cooper and R–V sites were 56 and 29 times more likely, respectively, to have *M. vimineum* present than not present, while plots experiencing a 1 unit decrease in tree seedling richness at the R–V sites were 62 times more likely to have *M. vimineum* than not present (Table 2).

Herb/shrub/vine richness ($\chi^2 = 41.22, P < 0.0001$) and diversity ($\chi^2 = 68.35$, $P < 0.0001$), tree seedling richness ($\chi^2 = 4.90$ $P = 0.027$) and diversity

Table 2 Logistic regression models with backwards selection and *M. vimineum* presence or absence as the binary response variable

Model	Site type	Adj R^2	AIC	Significant variables	χ	Odds ratio	95% CL
2005							
H–S–V diversity+[a]	Fernow ($N = 29$)	NA	NA	None	NA	NA	NA
T-S richness+	Cooper ($N = 31$)	0.51	29.04	H–S–V diversity	8.46	1.56	1.21–2.25
CWD + Total C	R–V ($N = 48$)	0.37	49.60	H–S–V diversity	6.01	1.29	1.07–1.62
				T-S richness	4.08	0.48	0.24–0.98
2006							
H–S–V richness+[b,c]	Fernow ($N = 91$)	0.26	110.86	H–S–V richness	7.46	1.24	1.07–1.46
T-S richness+				Canopy opening	5.35	1.22	1.05–1.46
Moss + CWD+	Cooper ($N = 83$)	0.63	69.28	H–S–V richness	18.49	2.53	1.73–4.08
Litter depth+				Litter depth	7.16	0.46	0.24–0.77
Canopy opening				Moss	5.87	1.36	1.11–1.84
+Light	R–V ($N = 77$)	0.54	73.58	H–S–V richness	8.56	2.13	1.34–3.71
				Canopy opening	4.22	1.28	1.03–1.65
				Moss	5.86	2.36	1.26–5.12
2007							
H–S–V richness+[d]	Fernow ($N = 137$)	0.08	179.43	H–S–V richness	7.50	1.20	1.06–1.38
T-S richness+	Cooper ($N = 109$)	0.35	123.91	H–S–V richness	17.65	1.74	1.37–2.30
Moss+				Light	5.21	1.06	1.02–1.12
Rock + Light				Moss	5.56	1.19	1.05–1.40
	R–V ($N = 95$)	0.46	94.15	H–S–V richness	20.62	3.06	1.99–5.25

H–S–V herb/shrub/vine, *T-S* tree seeding, *CWD* coarse woody debris, *CL* confidence limits, *AIC* Akaike information criterion, *NA* not applicable. Variables that make up the initial model were significant at the $P < 0.1$ level in separate generalized linear models. Diversity and richness variables could not be included in the same models due to multicollinearity

[a] The same model except with tree seedling diversity replacing tree seedling richness, produced similar results and is not presented

[b] The same model except with tree seedling diversity replacing tree seedling richness, produced similar results and is not presented

[c] The same model except with H–S–V diversity replacing H–S–V richness produced similar results and is not presented

[d] The same model except with H–S–V diversity replacing H–S–V richness produced similar results except moss and light were no longer significant for the Cooper site; this latter model is not presented

($\chi^2 = 5.46, P = 0.020$), canopy opening ($\chi^2 = 28.70$, $P < 0.0001$), light ($\chi^2 = 5.87, P = 0.015$), litter depth ($\chi^2 = 5.98$, $P = 0.015$), moss ($\chi^2 = 15.92$, $P < 0.0001$), and coarse woody debris ($\chi^2 = 8.92$ 12.36, $P = 0.003$) were all significant at $P < 0.1$ in the generalized linear models using 2006 data. Herb/shrub/vine richness and diversity and canopy opening were the most important variables of the logistic regression models for the Fernow sites, and the strongest model contained herb/shrub/vine diversity and canopy opening. Fernow plots with a 1 unit increase in herb/shrub/vine diversity and canopy opening were 963 and 20 times, respectively, more likely to have *M. vimineum* present than not present. Herb/shrub/vine diversity and richness were also significant for both the Cooper and R–V sites. Tree seedling richness and diversity were only significant for the R–V sites, with plots having lower seedling richness and diversity more likely to have *M. vimineum* present. Litter depth and moss cover were significant for the Cooper sites while canopy opening and moss were significant for the R–V sites. Cooper and R–V plots with a 1 unit increase in moss were 36 and 136 times, respectively, more likely to have *M. vimineum* present in 2006. Cooper plots with a 1 unit decrease in litter depth were 84 times more likely to have *M. vimineum* present than not present in 2006 (Table 2).

Herb/shrub/vine richness ($\chi^2 = 35.00, P < 0.0001$) and diversity ($\chi^2 = 58.35, P < 0.0001$), tree seedling richness ($\chi^2 = 2.72$, $P = 0.10$), moss ($\chi^2 = 2.38$, $P = 0.10$), rock ($\chi^2 = 10.00$, $P = 0.002$), and light ($\chi^2 = 7.37, P = 0.007$) were significant at $P < 0.1$ in the generalized linear models using 2007 data. Herb/shrub/vine richness and diversity were the most important variables of the logistic regression models. Moss and light were also significant but only for the Cooper plots in the model containing herb/shrub/vine richness. Fernow plots with a 1 unit increase in herb/shrub/vine diversity (the stronger of the two models) were 392 times more likely to have *M. vimineum* present in 2007. Cooper and R–V plots with a 1 unit increase in herb/shrub/vine richness were 74 and 206 times, respectively, more likely to have *M. vimineum* present. Cooper plots with a 1 unit increase in light and moss were 6 and 19 times, respectively, more likely to have *M. vimineum* present in 2007 (Table 2).

Herb/shrub/vine richness and diversity were the only variables that were important in the logistic regression models for every year and every site type, showing a positive correlation with the presence of *M. vimineum*. The importance of light, moss cover, canopy opening, and tree seedling richness and diversity varied with year and site type.

Discussion

These results support other findings, which show *M. vimineum* produces less biomass and fewer flowers and seed in low-light environments compared to populations in higher-light environments (Claridge and Franklin 2002; Cole and Weltzin 2005; Cheplick 2005). Nonetheless, while the three site types differed in terms of species richness and diversity, canopy opening, rock cover, litter depth, and moss cover, these differences did not correspond with a significant difference in average *M. vimineum* growth and reproduction by site. Thus, the local environmental gradient effects appear to impact *M. vimineum*'s successful establishment more than the regional gradient. Although no year-to-year statistical tests were conducted, stem heights were noticeably shorter at all sites in 2006, but less so in the Fernow sites, and cover decreased in 2007 in both the Cooper and R–V site types, perhaps in response to lower seed production in 2006. The year 2006 was a relatively dry in terms of August (when *M. vimineum* flowers are beginning to develop) precipitation for the Cooper (6.45 cm) and R–V (3.80 cm) sites compared to 2005 (Cooper = 7.67 cm, R–V = 9.88 cm) and 2007 (Cooper = 21.89 cm, R–V = 10.08 cm) and the Fernow sites (2005 = 12.15 cm, 2006 = 12.34, 2007 = 17.53 cm) (NOAA NCDC data). The change in precipitation may have also been reflected in the 2006 and 2007 moss cover in the more xeric R–V sites.

Herb/shrub/vine richness and diversity were the only variables that were consistently significant and were positively correlated with *M. vimineum* presence in interior plots across the regional gradient. Herb/shrub/vine richness and diversity may serve as surrogate measures of other resources such as soil moisture, light, and nutrients, which support the argument that both the native plants and *M. vimineum* respond similarly to the availability of abundant resources in these patches (Davis et al. 2000; Huebner and Tobin 2006). It is also possible that resources are not necessarily abundant in these patches but that niche partitioning among the species is occurring (Silvertown 2004). For instance, *M. vimineum* may utilize resources primarily in late summer, while many of the herbaceous understory species with which it is apparently coexisting likely utilize more resources in early and mid-summer. The roadside populations of *M. vimineum* appear to be competitively interacting with other plants, while *M. vimineum* in the forest interiors appear to be coexisting with other plants. A reduction in light abundance may be the trigger behind the shift from competition to coexistence along the local gradient.

Tree seedling richness and diversity revealed the opposite pattern across the gradient, with higher values in the forest interior plots compared to the roadside but lower values being associated with *M. vimineum* presence. Tree seedling cover and richness have been negatively correlated with herb cover and richness (Peet 1978; Huebner et al. 1995), and this interaction is typically attributed to competition between the herbs/shrubs/vines (resident species) and tree seedlings (transient species). The results of this paper indicate that tree seedlings may be somewhat competitive against *M. vimineum* in the forest interior. Jacques (2007) found that 2-year-old tree seedlings were more competitive than *M. vimineum* in both an open area and a thinned canopy with and without *M. vimineum* removal prior to planting the seedlings. The latter could indicate that maintaining a relatively healthy tree seedling bank in the understory may help reduce *M. vimineum* establishment in forest interiors.

What may be of most interest are the variables that did not define *M. vimineum* establishment in forest interiors consistently across time and the regional gradient, namely litter depth, moss cover, canopy closure, and light (PAR). Litter depth can vary temporally and it is conceivable that early fall measurements (prior to leaf senescence) may be less informative than a spring measurement would have been (when *M. vimineum* seedlings are first becoming established). However, spring measurements of all variables were taken in 2005 with no significant differences noted between spring and fall. Also, there is no doubt that canopy gaps or other disturbances that open the canopy facilitate the growth and reproduction of *M. vimineum* (Cole and Weltzin 2005; Glasgow and Matlack 2007), but the data presented here confirm that light gaps and obvious disturbances are not a requirement for establishment of *M. vimineum*. The amount of bare ground did show an insignificant trend of increasing over time, which may indicate an increase in small-scale disturbance such as water flow over the site or the inadvertent effects of data collection. While great efforts were taken not to disperse seed or disturb the sites when collecting the data, the simple act of walking in the sites may have been enough to increase the amount of bare ground. However, the increase in bare ground was not directly related to an increase in *M. vimineum* at these sites.

The importance of moss cover in 2006, the driest year, further manifests *M. vimineum*'s reliance on mesic conditions (Barden 1987; Redman 1995; Webster et al. 2008), but only in the more xeric sites of the regional gradient. Canopy opening was only important in terms of *M. vimineum* presence for the Fernow and R–V sites in 2006, though the Cooper sites had more open canopies (6.82%) than the Fernow (5.84%) and R–V (4.74%) sites this same year. Litter depth in 2006 was negatively associated with the presence of *M. vimineum*, which is supported by the literature (Oswalt and Oswalt 2007; Marshall and Buckley 2008b). However, this association only occurred in the Cooper sites, where litter was generally shallower (2.09 cm) than found at the Fernow (2.52 cm) and R–V (2.69 cm) sites in 2006. Canopy opening and litter depth are surrogate measures of disturbance. Plots in the most generally disturbed forest floor sites were more prone to invasion by *M. vimineum* if they had relatively shallow litter depths. In contrast, plots within sites with generally undisturbed canopies were more likely to be invaded if the plots were located just beneath a relatively more open canopy. These results may have helped define disturbance thresholds, i.e., canopy opening values above 6.8% and litter depths below 2.1 cm, at which point establishment of *M. vimineum* becomes more likely. Such thresholds may be evident only under more extreme environmental conditions, such as drier years.

The fact that *M. vimineum* average cover and stem counts per 1-m^2 (in plots containing *M. vimineum*) do not vary across the regional gradient indicates *M. vimineum* seed will germinate and grow in any safe patch (one that is apparently preferred by several native herb species too), even in more xeric sites along the moisture gradient. However, these data do not tell us if *M. vimineum* is less likely to colonize and spread under more stressful conditions in which one would assume there are fewer safe patches available. The next paper (by the same author) addresses the question of *M. vimineum* population growth and spread over both local and regional gradients.

Acknowledgements The USDA Forest Service funded this research. I thank H. Smith, M. McKissik, W. Laubscher, G. Short, J. Quinn, and L. Strickler for their help in data collection. We also thank P. Tobin, J. Stanovick, D. Simberloff, and two anonymous reviewers for their editorial comments.

References

Baiser B, Lockwood JL, LaPuma D, Aronson MFJ (2008) A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biol Invasions 10:785–795

Barden LS (1987) Invasion of *Microstegium vimineum* (Poaceae), an exotic, annual, shade-tolerant, C_4 grass, into a North Carolina floodplain. Am Midl Nat 118:40–45

Begon M, Harper JL, Townsend CR (1996) Ecology—individuals, populations, and communities, 3rd edn. Blackwell Science, Oxford, UK, 1068 pp

Bradford MA, DeVore JL, Maerz JC, McHugh JV, Smith CL, Strickland MS (2009) Native, insect herbivore communities derive a significant proportion of their carbon from a widespread invader in forest understories. Biol Invasions. doi:10.1007/s10530-009-9480-x

Brown JS (2000) Foraging ecology of animals in response to heterogeneous environments. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. Cambridge University Press, London, UK, pp 181–213

Chazdon R, Pearcy RW (1991) The importance of sunflecks for forest understory plants. Bioscience 41(11):760–766

Cheplick GP (2005) Biomass partitioning and reproductive allocation in the invasive, cleistogamous grass *Microstegium vimineum*: influence of the light environment. J Torrey Bot Soc 132:214–224

Civitello DJ, Flory SL, Clay K (2008) Exotic grass invasion reduces survival of *Amblyomma americanum* and *Dermacentor variabilis* ticks (Acari: Ixodidae). J Med Entomol 45:867–872

Claridge K, Franklin SB (2002) Compensation and plasticity in an invasive plant species. Biol Invasions 4:339–347

Clarkson RB (1964) Tumolt on the mountains—lumbering in West Virginia—1770–1920. McClain Printing Company, Parsons, WV, 402 pp

Cole PG, Weltzin JF (2004) Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in East Tennessee. Southeast Nat 3:545–562

Cole PG, Weltzin JF (2005) Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. Biol Invasions 7:477–488

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Ehrenfeld JG, Kourtev P, Huang W (2001) Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecol Appl 11:1287–1300

Eschtruth AK, Battles JJ (2008) Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conserv Biol 23(92):388–399

Eschtruth AK, Cleavitt NL, Battles JJ, Evans RA, Fahey TJ (2006) Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Can J For Res 36:1435–1450

Fairbrothers DE, Grayt JR (1972) *Microstegium vimineum* (Trin.) A. Camus (Graminaceae) in the United States. Bull Torrey Bot Club 99:97–105

Fitter A, Hodge A, Robinson D (2000) Plant response to patchy soils. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. Cambridge University Press, London, UK, pp 71–179

Gibson DJ, Spyreas G, Benedict J (2002) Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. J Torrey Bot Soc 129:207–219

Gilbert B, Lechowicz MJ (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology 86(7):1848–1855

Glasgow LS, Matlack GR (2007) The effects of prescribed burning and canopy openness on establishment of two non-native plant species in a deciduous forest, southeast Ohio, USA. For Ecol Manag 238:319–329

Gleason HA, Cronquist A (1993) Manual of vascular plants of northeastern United States and adjacent Canada, 2nd edn. The New York Botanical Garden, Bronx, NY, 910 pp

Global Invasive Species Database (2008) http://www.issg.org/database/welcome/. Last Accessed December

Griggs JA, Rock JH, Webster CR, Jenkins MA (2006) Vegetative legacy of a protected deer herd in Cades Cove, Great Smoky Mountains National Park. Nat Areas J 26:126–136

Horton JJ, Neufeld HS (1998) Photosynthetic responses of *Microstegium vimineum* (Trin.) A. Camus, a shade-tolerant, C_4 grass, to variable light environments. Oecologia 114:11–19

Huebner CD (2003) Vulnerability of oak-dominated forests in West Virginia to invasive exotic plants: temporal and spatial patterns of nine exotic species using herbarium records and land classification data. Castanea 68:1–14

Huebner CD (2007) Strategic management of five deciduous forest invaders using *Microstegium vimineum* as a model species. In: Cavender N (ed) Proceedings of the Ohio invasive plants research conference: continuing partnerships for invasive plant management. Ohio Biological Survey, Columbus, OH, pp 19–28

Huebner CD, Tobin PC (2006) Invasibility of mature and 15-year-old deciduous forests by exotic plants. Plant Ecol 186:57–68

Huebner CD, Randolph JC, Parker GR (1995) Environmental factors affecting understory diversity in second-growth deciduous forests. Am Midl Nat 134:155–165

Integrated Taxonomic Information System (ITIS) (2008) Retrieved from http://www.itis.gov/ on 2 December

Jacques RR (2007) Effects of *Microstegium vimineum* (Trin.) A. Camus (Asian stiltgrass; Poaceae) on native hardwood seedling growth and survival. Master of Science thesis, Department of Environmental and Plant Biology Ohio University, Athens, OH, 47 pp

Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638

Kourtev P, Ehrenfeld JG, Huang W (1999) Differences in earthworm densities and nitrogen dynamics under exotic and native plant species. Biol Invasions 1:237–245

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

Marshall JM, Buckley DS (2008a) Effects of microsites created by selective harvesting on growth of *Microstegium vimineum* in a Central Hardwood forest. For Sci 54:534–542

Marshall JM, Buckley DS (2008b) 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

Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasioins: intentional introductions, stand dynamics, and the role of shade tolerance. Front Ecol Environ 7(3):142–149

McGrath DA, Binckley MA (2009) *Microstegium vimineum* invasion changes soil chemistry and microarthropod communities in Cumberland Plateau forests. Southeast Nat 8(1):141–156

NOAA National Climate Center Data (NCDC) (2008) Retrieved from http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~SelectStation~USA~WV on 3 December

Orwig DA, Foster DR (1998) Forest response to the introduced hemlock woolly adelgid in southern New England, USA. J Torrey Bot Soc 125:60–73

Oswalt CM, Oswalt SN (2007) Winter litter disturbance facilitates the spread of the nonnative invasive grass *Microstegium vimineum* (Trin.) A. Camus. For Ecol Manag 249:199–203

Oswalt CM, Oswalt SN, 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. For Ecol Manag 242:727–732

Pausas JG, Austin MP (2001) Patterns of species richness in relation to different environments: an appraisal. J Veg Sci 12:153–166

Peet RK (1978) Forest vegetation of the Colorado front range: patterns of species diversity. Vegetatio 37:65–78

Pickett STA, Bazzaz FA (1976) Divergence of two co-occurring successional annuals on a soil moisture gradient. Ecology 57:169–176

Pyšek P, Jarošík V, Kučera T (2002) Patterns of invasion in temperate nature reserves. Biol Conserv 104:13–24

Radosevich SR, Stubbs MM, Ghersa CM (2003) Plant invasions–process and patterns. Weed Sci 51:254–259

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

Richardson DM, Williams PA, Hobbs RJ (1994) Pine invasions in the Southern Hemisphere: determinants of spread and invadability. J Biogeogr 21:511–527

Scholz H, Byfield AJ (2000) Three grasses new to Turkey. Turk J Bot 24:263–267

Silvertown J (2004) Plant coexistence and the niche. Trends Ecol Evol 19:605–611

Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M, Son Y (1999) Exotic plant species invade hot spots of native plant diversity. Ecol Monogr 69:25–46

Tanaka H (1975) Pollination of some Gramineae (2). J Jpn Bot 50:25–31

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92

Urban DL, Miller C, Halpin PN, Stephenson NL (2000) Forest gradient response in Sierran landscapes: the physical template. Landscape Ecol 15:603–620

Webster CR, Rock JH, Froese RE, Jenkins MA (2008) Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum,* 10-year results. Oecologia 157:497–508

West Virginia Department of Agriculture (2008) Retrieved from http://www.wvagriculture.org/images/Plant_Industries/Rules_Dealing_With_Noxious_Weeds08.pdf on 30 November

Winter K, Schmitt MR, Edwards GE (1982) *Microstegium vimineum*, a shade adapted C_4 grass. Plant Sci Lett 24:311–318