

Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus¹

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LEICHT, S. A., J. A. SILANDER JR., AND K. GREENWOOD (University of Connecticut, Department of Ecology and Evolutionary Biology, 75 North Eagleville Rd. U-3043, Storrs, CT 06269). Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus. J. Torrey Bot. Soc. 132: 573–580. 2005—*Microstegium vimineum* (Japanese stilt grass) is an invasive grass in the eastern half of the United States which can form dense monocultures in forest understories, displacing native species. Although the loss of native species has been observed in the field, the actual competitive ability of this grass has not been examined. *Microstegium vimineum* was grown under controlled environment, greenhouse conditions in competition with *Lolium perenne* ssp. *multiflorum* (annual rye grass) and *Muhlenbergia mexicana* (Mexican muhly) in varying density ratios in full and low light treatments. *Microstegium vimineum* had a greater aboveground biomass, relative growth rate, and reproductive output than both competitors in both light treatments. The high competitive ability of *Microstegium vimineum*, especially in low light conditions, reflects its highly aggressive nature in forested or other landscapes of eastern North America.

Key words: annual rye grass, competition, invasive species, Japanese stilt grass, *Lolium perenne* ssp. *multiflorum*, *Microstegium vimineum*, *Muhlenbergia mexicana*.

Microstegium vimineum (Trin.) A. Camus (Japanese stilt grass, hereafter referred to as *Microstegium*) is an invasive annual grass introduced into the United States from Asia. The earliest record of this plant in the United States is from Knoxville, Tennessee in 1919 (Fairbrothers and Gray 1972). Since this 1919 introduction, it has spread rapidly to the northeast, reaching New Jersey by 1959 (Fairbrothers and Gray 1972). By 1984, *Microstegium* was reported in Branford, Connecticut and in Hampden, Massachusetts by 1998 (Mehrhoff et al. 2003). In fact, new records in New England for this plant are being reported monthly (Mehrhoff pers. comm.). There is some question as to how far north this species can continue its spread, as the extent of its cold tolerance is unknown (Hunt and Zaremba 1992). Seedlings can be killed back by a late spring frost; however, more plants

will germinate from the seed bank to replace these (Barden 1987).

Throughout its range, *Microstegium* is found in a variety of habitats such as floodplains, thickets, lawns, mesic forests, meadows, stream-sides, utility rights-of-way, logging roads and roadsides (Fairbrothers and Gray 1972, Hunt and Zaremba 1992; Redman 1995). Even though this plant is a C₄ grass, it is shade-tolerant, allowing it to invade in the forest understory (Winter et al. 1982, Horton and Neufeld 1998). In the forest understory, it is able to form dense swards, which are detrimental to native plant species (Hunt and Zaremba 1992, Ehrenfeld 1999, Mehrhoff 2000). Individual *Microstegium* plants can produce 100–1000 seeds (Gibson et al. 2002) and exist at densities of 3000–4000 plants per m² (Barden 1996). The *Microstegium* seed bank can survive more than three years (Barden 1987).

Since *Microstegium* most commonly invades where there has been a disturbance to the vegetation (Williams 1998), *Microstegium* and other native species will be regenerating together, presumably in competition with each other. The purpose of this study was to determine the ability of *Microstegium* to compete with other grass species using complete additive design, two-species competition experiments (Silvertown and Charlesworth 2001). Previous studies have shown that *Microstegium* is able to rapidly infiltrate disturbed sites, but it was slow to invade monocultures of another aggressive invasive

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plant, *Lonicera japonica* (Barden 1987). However, where *Microstegium* has invaded at high densities, the biomass of other species has been very low or zero (Williams 1998).

We chose two grasses with different life-histories to compete against *Microstegium* in both sun and shade conditions. One was *Lolium perenne* ssp. *multiflorum* (Lam.) Husnot (Annual rye grass, hereafter referred to as *Lolium*) and the other was *Muhlenbergia mexicana* (L.) Trin. (Mexican muhly, hereafter referred to as *Muhlenbergia*). *Lolium* was chosen because it is one of the most rapidly-growing annual grass species, often used to quickly and aggressively establish lawns under a variety of conditions. Consequently, *Lolium* has commonly selected for competition experiments (Harper 1977). This species is naturalized in meadows and other open areas (Gleason and Cronquist 1991) and is an aggressive invasive species in parts of the United States (Marañón and Bartolome 1993). *Lolium* is similar to *Microstegium* in that it has an annual life-history, but is a C₃ plant. *Muhlenbergia mexicana* was selected because this genus has been observed growing with *Microstegium* (Redman 1995). *Muhlenbergia* is found in moist or wet habitats and can occur in both open and forested areas (Gleason and Cronquist 1991). This species has a perennial life history, and like *Microstegium*, *Muhlenbergia* is a C₄ plant.

We tested the hypothesis that *Microstegium* would be the better competitor against *Lolium* and *Muhlenbergia* as measured in weight per plant, relative growth rate (RGR) and reproductive output. However, we expected that the success of *Microstegium* would be more pronounced in the shade treatment than in the sun, since its success in the forest understory has been well documented (Winter et al. 1982, Hunt and Zaremba 1992, Redman 1995, Barden 1996, Horton and Neufeld 1998).

Materials and Methods. This study was conducted in the University of Connecticut research greenhouses in spring 2002 and spring 2003. The competition experiment between *Lolium* and *Microstegium* ran from April 2002 to May 2002. This experiment concluded when *Lolium* began to set seed and before the *Microstegium* fruited so that the seeds of *Microstegium* would not be spread. There have been instances of other species escaping and spreading not only within the greenhouse but into natural systems (Leicht, pers. obs.). An additional

experiment with *Muhlenbergia* and *Microstegium* was conducted from March 2003 to May 2003. In this experiment, precautions were taken (isolation of the greenhouse, etc.) in order to collect data on reproduction. In both experiments, seeds were germinated in trays and then transplanted into the experimental pots at the two-leaf stage. *Microstegium* and the competitor (*Lolium* or *Muhlenbergia*) were potted together in 70, 12.7-cm square pots in different density ratios in two light treatments. The full light treatment in the greenhouse was 100 percent ambient light (peak photosynthetically active radiation (PAR) $\approx 406.9 \mu\text{mol m}^{-2} \text{s}^{-1}$, about 45% full sun) and the low light treatment was 37 percent transmittance of ambient light ($\approx 152.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ or about 9% full sun). The shade treatment was created through the use of 70 percent shade Aluminet shade cloth (Green-Tek, Edgerton, WI). These light measurements confirmed using a LICOR 170SA quantum sensor. The soil used was a loam-sand-peat custom mix selected to emulate natural conditions. Plants were watered using a drip irrigation system such that all pots received the same amount of water and nutrients. Plants were on a continuous liquid feed using 20–20–20 Scotts Peters General purpose fertilizer at 125 ppm N with periodic clear water leaching. The densities in the pots were as follows (*Microstegium*:competitor): 0:1, 0:5, 0:10, 0:20, 0:30, 1:0, 1:1, 1:5, 1:10, 1:20, 1:30, 5:0, 5:1, 5:5, 5:10, 5:20, 5:30, 10:0, 10:1, 10:5, 10:10, 10:20, 10:30, 20:0, 20:1, 20:5, 20:10, 20:20, 20:30, 30:0, 30:1, 30:5, 30:10, 30:20, 30:30. Seedlings that died from transplant shock during the first two weeks were replaced by comparably-sized seedlings. After two weeks had passed, seedlings were no longer replaced since mortality was likely caused at this point by competition for resources and not transplant shock.

At the beginning of the experiment, we measured the height of three randomly selected plants per pot. These same three plants were measured again at the end of the experiment. Using the height measurements, the relative height growth rate ($\text{RGR}_{\text{height}}$) of the plants was calculated using the following equation:

$$\text{RGR}_{\text{height}} = \frac{\ln \text{height}_{\text{final}} - \ln \text{height}_{\text{initial}}}{\text{time}_{\text{final}} - \text{time}_{\text{initial}}}$$

The $\text{RGR}_{\text{height}}$ of the three individual plants (when there were three available) per pot were averaged and used in the analysis. $\text{RGR}_{\text{height}}$ has been used in previous studies to compare native

and invasive species growth rates (e.g., Sanford et al. 2003).

At the end of the *Microstegium* and *Muhlenbergia* experiment, we harvested and counted the reproductive spikes in order to assess reproductive potential (Claridge and Franklin 2002, Gibson et al. 2002). Finally, individual plants were clipped at soil level, separated by species and counted. These samples were oven dried and weighed in order to determine aboveground biomass. Mean weight in grams per plant was determined by weighing all of the plants in the sample, and dividing by the number of individuals present. This measure (mean weight per plant) has been used as a measure of yield (in this case, biomass) in a variety of studies (Silvertown and Charlesworth 2001).

Biomass yield per plant was modeled as a function of density using non-linear regression, following Firbank and Watkinson (1985):

$$w_{\text{micro}} = w_{\text{mmicro}} [1 + a_{\text{micro}} (N_{\text{micro}} + \alpha_{\text{micro,comp}} N_{\text{comp}})]^{b_{\text{micro}}}$$

$$w_{\text{comp}} = w_{\text{mcomp}} [1 + a_{\text{comp}} (N_{\text{comp}} + \alpha_{\text{comp,micro}} N_{\text{micro}})]^{b_{\text{comp}}}$$

where w_{micro} or w_{comp} is the mean yield per plant, w_{mmicro} or w_{mcomp} is the maximum yield of one, isolated plant, a is the approximate area (in m^2) needed by one plant to achieve w_m , N is the density of the plants, $\alpha_{\text{micro,comp}}$ is the competition coefficient for the affect of the competitor species on *Microstegium* while $\alpha_{\text{comp,micro}}$ represents the effect of the *Microstegium* on the competitor and b is a fitting parameter for the curve (Watkinson 1980). The subscripts "micro" and "comp" represent *Microstegium* and the competitor (*Lolium* or *Muhlenbergia*) respectively. We determined if the competition coefficient was different than one by examining the standard errors of the coefficients to see if they overlapped one.

The $\text{RGR}_{\text{height}}$ data were first analyzed with a linear regression to determine if there was an effect of total plant density on growth rate. Additionally, we grouped the data together and used two-sample t-tests to compare the $\text{RGR}_{\text{height}}$ of the grass species. $\text{RGR}_{\text{height}}$ was compared within a species in order to determine if that species had a higher $\text{RGR}_{\text{height}}$ in the low or high light treatment. $\text{RGR}_{\text{height}}$ was also compared across species to determine which species had the greater $\text{RGR}_{\text{height}}$. We examined the number of reproductive spikes as a function of density using linear regression. After determining that

density did not affect the number of reproductive spikes, we pooled the data together and used two-sample t-tests to compare the reproductive output within species in the two different light treatments as well as across species in the same light treatment. All analyses were conducted in S-PLUS 6.1 (Insightful Corporation 2002).

Results. BIOMASS OF GRASS SPECIES. All of the grass species showed a decrease in biomass per plant with increasing numbers of plants per pot (Figures 1a–d, 2a–d). However, not all of the regression surfaces were smooth, and showed variation in plant weights (e.g., Figure 2b). The results of the non-linear regression for the *Microstegium* vs. *Lolium* and *Microstegium* vs. *Muhlenbergia* competitions are summarized in Table 1 and illustrated in Figures 3a–d. All of the plant weights (g/plant) reached an asymptote when plant density no longer impacts the yield (Figure 3a–d). For all three species, plants in the sun treatments always had a greater biomass than those plants grown in the shade (Figure 3a–d). Additionally, *Microstegium* had greater weight per plant than either *Lolium* or *Muhlenbergia*. In the light treatments, *Microstegium* was significantly more competitive than *Lolium* ($P = 0.002$, Figure 3a) and *Muhlenbergia* ($P = 0.03$, Figure 3c). In the shade treatments, the competition coefficients had confidence intervals that overlapped one for both the *Microstegium* vs. *Lolium* competition (Figure 3a, 3b the dashed lines) as well as the *Microstegium* vs. *Muhlenbergia* competition (Figure 3c, 3d the dashed lines).

COMPETITION COEFFICIENTS. The competition coefficients from Table 1 can be interpreted as follows: if the value of $\alpha_{\text{comp,micro}} > 1$ then *Microstegium* has a greater effect on the competitor species (*Lolium* or *Muhlenbergia*) than *Microstegium* has on itself (interspecific competition). Conversely, if $\alpha_{\text{comp,micro}} < 1$, then *Microstegium* is more strongly effected by itself than by the competitor (intraspecific competition). Finally, if $\alpha_{\text{comp,micro}} \approx 1$ then the interspecific and intraspecific effects are approximately equal. For example, in the light treatment, the competition coefficient indicated that *Microstegium* had 9.6 times the effect on the biomass yield of *Muhlenbergia* as *Muhlenbergia* plants had on each other. In the shade treatment, interspecific interactions were greater overall, but the effects of *Microstegium* and *Muhlenbergia* on each other were more similar. For *Lolium*, the competition

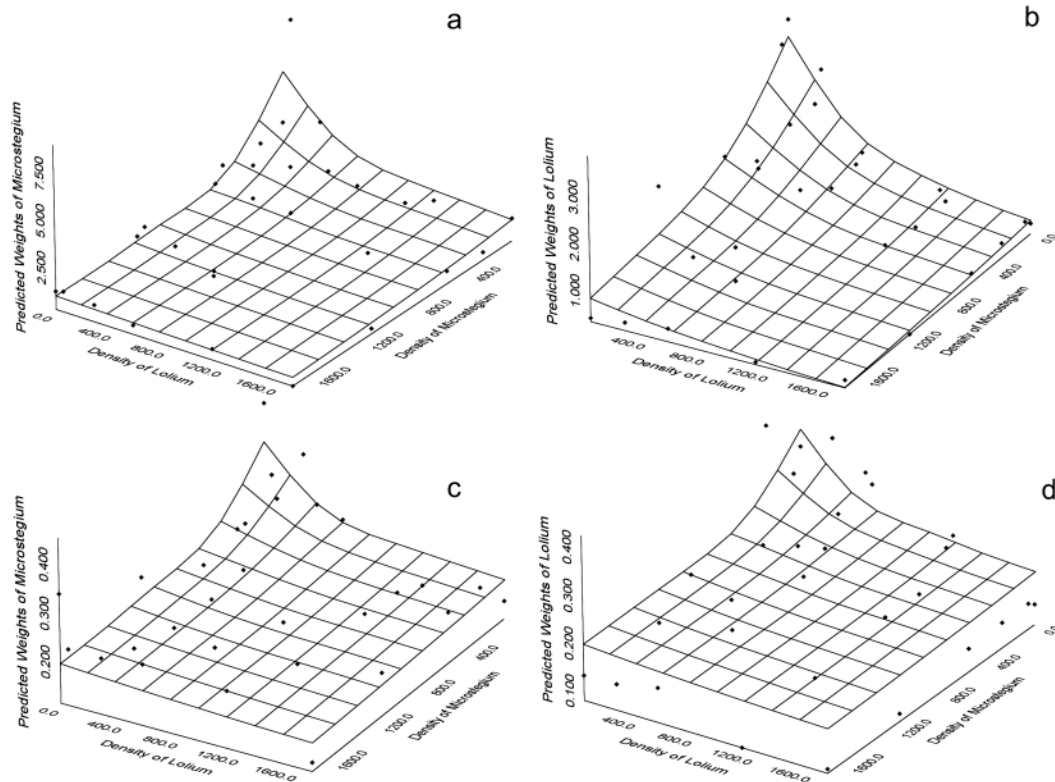


FIG. 1a–d. Regression surfaces for *Microstegium* vs. *Lolium* competition experiments. (a) Predicted weights of *Microstegium* vs. the densities of *Lolium* and *Microstegium* (plants/m²), full light treatment. $w_{\text{micro}} = 9.18 [1 + 0.015(N_{\text{micro}} + 0.054N_{\text{lolium}})]^{-0.614}$. $R^2 = 0.5993$. (b) Predicted weights of *Lolium* vs. the densities of *Lolium* and *Microstegium* (plants/m²), full light treatment. $w_{\text{lolium}} = 3.92 [1 + 0.002(N_{\text{lolium}} + 0.724N_{\text{micro}})]^{-1.202}$. $R^2 = 0.7604$. (c) Predicted weights of *Microstegium* vs. the densities of *Lolium* and *Microstegium* (plants/m²), low light treatment. $w_{\text{micro}} = 0.46 [1 + 0.054(N_{\text{micro}} + 0.910N_{\text{lolium}})]^{-0.197}$. $R^2 = 0.3412$. (d) Predicted weights of *Lolium* vs. the densities of *Lolium* and *Microstegium* (plants/m²), low light treatment. $w_{\text{lolium}} = 0.43 [1 + 0.011(N_{\text{lolium}} + 1.347N_{\text{micro}})]^{-0.358}$. $R^2 = 0.6524$.

coefficients were smaller, with both $\alpha_{\text{comp, micro}}$ and $\alpha_{\text{micro, comp}}$ being < 1 in the light and slightly higher than one in the shade (Table 1).

RGR_{height} OF GRASS SPECIES. An examination of species specific RGR_{height} of the plants revealed that *Lolium* ($R^2 = 0.33$, $P = 0.0009$) grown in the light and *Muhlenbergia* ($R^2 = 0.45$, $P < 0.0001$) in the shade treatment showed decreased RGR_{height} with increasing density. In competition with *Lolium*, *Microstegium* had a significantly higher RGR_{height} in the light than in the shade treatment ($P < 0.0001$). *Lolium* on the other hand, did not show a significant difference in RGR_{height} between light and shade grown treatments. However, when the two species were compared to each other, *Microstegium* had a significantly higher RGR_{height} than *Lolium* in the light ($P < 0.0001$) as well as in the shade ($P < 0.0001$) treatments.

The RGR_{height} of *Microstegium* grown in the light did not differ from that of *Microstegium* grown in the shade ($P = 0.91$). *Muhlenbergia* showed a similar trend, with no significant difference in RGR_{height} between *Muhlenbergia* grown in shade and *Muhlenbergia* grown in light ($P = 0.14$). However, *Microstegium* had significantly higher RGR_{height} than *Muhlenbergia* in both the light ($P < 0.0001$) and shade treatments ($P < 0.0001$).

REPRODUCTIVE POTENTIAL. The reproductive potential expressed as number of reproductive spikes, was significantly higher in *Microstegium* ($\bar{x} = 130$, SE = 17.4) than in *Muhlenbergia* ($\bar{x} = 45$, SE = 8.5) in the light ($P < 0.0001$) treatment. *Microstegium* ($\bar{x} = 61$, SE = 9.8) also had a greater number of reproductive spikes than *Muhlenbergia* ($\bar{x} = 0.5$, SE = 0.2) in the shade ($P < 0.0001$) treatment. When the reproductive

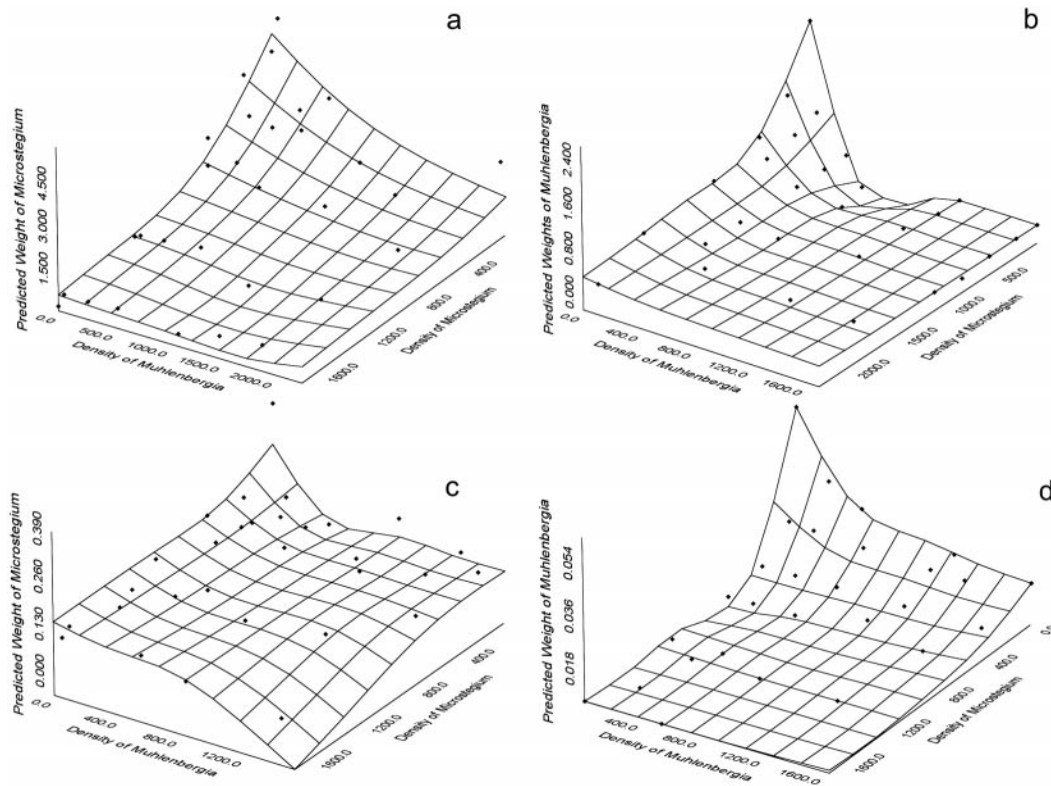


FIG. 2a–d. Regression surfaces for *Microstegium* vs. *Muhlenbergia* competition experiments. (a) Predicted weights of *Microstegium* vs. the densities of *Muhlenbergia* and *Microstegium* (plants/m²), full light treatment. $w_{\text{micro}} = 5.9 [1 + 0.001 (N_{\text{micro}} + 0.356N_{\text{muhl}})]^{-2.312}$, $R^2 = 0.8950$. (b) Predicted weights of *Muhlenbergia* vs. the densities of *Muhlenbergia* and *Microstegium* (plants/m²), full light treatment. $w_{\text{muhl}} = 3.44 [1 + 0.0063(N_{\text{muhl}} + 9.57N_{\text{micro}})]^{-0.77}$, $R^2 = 0.7719$. (c) Predicted weights of *Microstegium* vs. the densities of *Muhlenbergia* and *Microstegium* (plants/m²), low light treatment. $w_{\text{micro}} = 0.4 [1 + 0.122 (N_{\text{micro}} + 17.9N_{\text{muhl}})]^{-0.18}$, $R^2 = 0.3438$. (d) Predicted weights of *Muhlenbergia* vs. the densities of *Muhlenbergia* and *Microstegium* (plants/m²), low light treatment. $w_{\text{muhl}} = 0.1 [1 + 0.048(N_{\text{muhl}} + 23.07N_{\text{micro}})]^{-0.33}$, $R^2 = 0.5251$.

Table 1. Estimated parameters from non-linear regression for competition of *Microstegium* vs. *Lolium* and *Muhlenbergia*.

Competition	Estimated coefficients					
	$\alpha_{\text{comp,micro}}$	$\alpha_{\text{micro,comp}}$	a_{micro}	a_{comp}	b_{micro}	b_{comp}
<i>Microstegium</i> vs. <i>Lolium</i> (Light)	0.724*	0.054*	0.015	0.002	-0.614	-1.202
<i>Microstegium</i> vs. <i>Lolium</i> (Shade)	1.347	0.910	0.054	0.011	-0.197	-0.358
<i>Microstegium</i> vs. <i>Muhlenbergia</i> (Light)	9.574*	0.357*	0.001	0.006	-2.313	-0.774
<i>Microstegium</i> vs. <i>Muhlenbergia</i> (Shade)	23.070	17.919	0.122	0.049	-0.181	-0.333

Boldface values indicate significance at the $P \leq 0.05$ level. a is the approximate area (m²) needed by one plant to achieve maximum weight, $\alpha_{\text{comp,micro}}$ represents the effect of the *Microstegium* on the competitor while $\alpha_{\text{micro,comp}}$ is the competition coefficient for the effect of the competitor on *Microstegium* and b is a fitting parameter for the curve. An * indicates competition coefficients whose standard errors do not overlap 1.

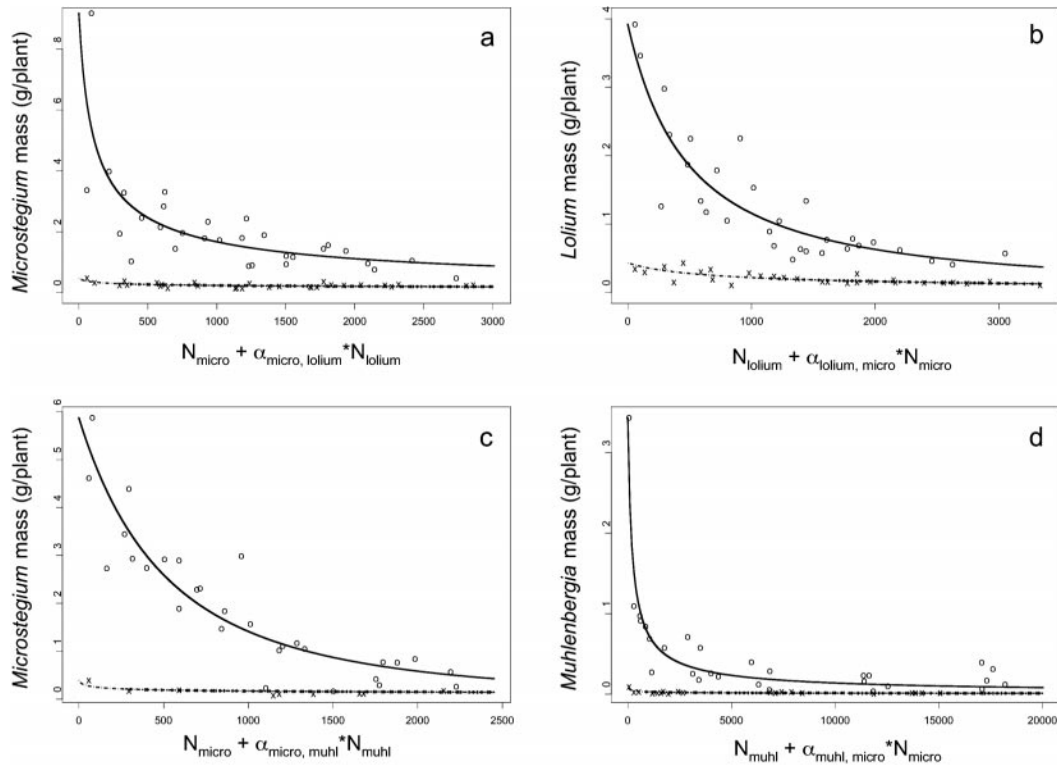


FIG. 3a–d. Non-linear regressions for competition experiments. Figures 3a and 3b are from the *Microstegium* vs. *Lolium* experiment and Figures 3c and 3d are from the *Microstegium* vs. *Muhlenbergia* experiment. On the y-axis are the weights of the plants in g/plant. On the x-axis is the “competitive intensity” as expressed as $N_{\text{micro}} + \alpha_{\text{micro, comp}} * N_{\text{comp}}$ or $N_{\text{comp}} + \alpha_{\text{comp, micro}} * N_{\text{micro}}$. Competitive intensity is the sum of the number of the intraspecific competitors to the product of the number of interspecific competitors and the competition coefficient. The subscript, “micro” = *Microstegium* and comp = “lolium” or “muhl” for *Lolium* and *Muhlenbergia* respectively. In each graph, the “o” represents points from the full light treatment and “x” represents points from the low light treatment. Equations for the non-linear regression are as shown in Figures 1a–d and 2a–d.

potential of *Microstegium* was compared in the light versus the shade treatment, *Microstegium* grown in the light had significantly more spikes than those grown in the shade ($P = 0.001$). Finally, *Muhlenbergia* grown in the light had significantly more spikes than those grown in the shade ($P < 0.0001$).

Discussion. *Microstegium* has been implicated in the crowding out of native plant species (Redman 1995, Williams 1998); however, its actual competitive ability had not previously been inspected (Claridge and Franklin 2002). The present study examined the ability of *Microstegium* to compete against two grasses with different life-histories. In previous field experiments, greater biomass of interspecific neighbors was associated with reduced biomass of *Microstegium* in high light situations (Williams 1998). Intraspecific competition also reduced *Micro-*

stegium reproductive output (Williams 1998). All of the grass species in this study showed a decrease in individual plant biomass with increasing density. This result is not surprising given the law of constant final yield which states that plants are negatively effected with increasing density, but eventually reach an asymptote at which their yield (in this case, biomass) remains constant (Kira et al. 1953, Harper 1977).

Microstegium was able to outcompete both of the other grass species. However, the competitive ability of *Microstegium* was different depending on the species it was grown with. In two out of the four competitive scenarios, the effect of *Microstegium* on the competitor is greater than the effect the competitor had on itself (*i.e.*, $\alpha_{\text{comp, micro}} > 1$). This effect of *Microstegium* is substantial, with the competition coefficient ($\alpha_{\text{comp, micro}}$) being as much as 27 times higher than the ($\alpha_{\text{micro, comp}}$), suggesting strong asym-

metric competition. These large interspecific competition coefficients indicate that *Microstegium* will likely outcompete the other two species for resources. In order for *Lolium* or *Muhlenbergia* to be able to compete with the invasive grass, the production of seeds or survival of juvenile plants would have to be much greater than that of *Microstegium*.

Microstegium has a variety of life-history traits that make it a good competitor. The higher RGR_{height} of *Microstegium* implies that it will grow faster in height than its competitors, although its final height may not be greater than its competitors. In the *Microstegium* vs. *Muhlenbergia* experiment there was no difference in the RGR_{height} of *Microstegium* in the light and shade treatments. The ability of this plant to grow at similar rates in the light and shade points a plastic physiology of *Microstegium* (Claridge and Franklin 2002, Gibson et al. 2002). Understanding the plasticity of *Microstegium* is key to understanding its success. The ability of *Microstegium* to maintain its final height in both the sun and shade in previous studies was attributed to additional aboveground allocation to stems and leaves, compensating for the shading (Claridge and Franklin 2002).

In terms of the relationship of aboveground biomass to light treatment, we found a negative effect of decreased light on biomass of *Microstegium*. These results agree with those of Claridge and Franklin (2002), who also found a significant decrease in biomass under 2–7 percent of full light in the greenhouse. In contrast, Winter et al. (1982) found no effect of light levels on *Microstegium* biomass. Even under 5 percent of sun, *Microstegium* was capable of positive growth, while the other C_4 grass species examined were unable to grow under these conditions (Winter et al. 1982). The other C_4 species in our experiment, *Muhlenbergia*, which like *Microstegium*, can be found in shaded conditions. In another study, *Muhlenbergia* species also survived in the shade but attained greater biomass in high light conditions (Smith and Martin 1987).

Two-species plant competition experiments have been used in the past to evaluate the effect of weed species on crops (Rejmánek et al. 1989, Pantone and Baker 1991). The competition coefficients such as those reported here could allow us to quantify how much of an effect invasive species are having on their native neighbors. The first step in modeling these competitive interactions is most effectively done in a

greenhouse setting. This step lays the groundwork for understanding how *Microstegium* interacts with other species. The next logical step is to conduct competition experiments in the field in a natural setting. This is critical because the driving forces that affect the outcome of competition may be a suite of other environmental factors in addition to light availability (e.g. temperature regimes, soil moisture and other edaphic factors). Field experiments would help in predicting how *Microstegium* would spread if it were able to colonize an area already dominated by native species. However, in the case of this study, the danger of spread of *Microstegium* into a landscape where it is largely absent posed too high a risk to undertake the field trials. Further work on the mechanisms which allow *Microstegium* to be such a superior competitor needs to be conducted in order to develop strategies for preventing the further spread of this species into new locations in the Northeast and elsewhere in the United States.

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