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Experimental Light Treatments Affect Invasion Success and the Impact of *Microstegium vimineum* on the Resident Community

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ABSTRACT: In forests of the eastern United States, exotic plant invasions can reduce native plant diversity and change ecosystem processes. Many invasive plants colonize forest edge habitat, but little is known about the ability of the exotic annual grass *Microstegium vimineum* to invade edges compared to interior forest. In particular, the extent of invasion and impact on resident plants might change along the environmental gradient from edge to interior sites. A common garden study was used to test how *Microstegium* invasion affected six forest understory graminoid species across three experimental light treatments. Contamination of the *Microstegium* seed stock with seed of the dominant native perennial grass *Dichanthelium clandestinum* provided the opportunity to study the interaction between the two species across the light treatments. The light treatments shifted the competitive balance between *Microstegium* and *Dichanthelium*, with *Dichanthelium* dominating in full sun, *Microstegium* dominating in full shade, and the two species producing more similar biomass in part shade. Invasion of resident communities by these two species resulted in a significant reduction in resident community biomass in part shade but not in full sun or full shade. Three of the six resident graminoid species produced significantly less biomass under invaded conditions. Successful management of *Microstegium* will require that land managers monitor partly shaded and fully shaded forests to locate invading populations. Invasions should be treated quickly to minimize impacts on resident community species.

Index terms: *Dichanthelium*, exotic species, forest edge, forest interior, shade

INTRODUCTION

Invasions of exotic plants can reduce native biodiversity (Merriam and Feil 2002) and alter fundamental ecosystem processes (e.g. Cronk and Fuller 1995; Mack et al. 2000; Blossey et al. 2001; Titus and Tsuyuzaki 2003) in both natural and managed systems in the United States. Two fundamental issues in invasion ecology are: (1) determining where exotic plants are able to invade and (2) how they impact resident plant communities (Reichard and Hamilton 1997; Kolar and Lodge 2001; Meiners et al. 2001; Merriam and Feil 2002; Gorchov and Trisel 2003).

Eastern deciduous forests in the United States have been invaded by numerous woody and herbaceous exotic plant species (e.g. Hutchinson and Vankat 1997; Goldblum and Beatty 1999). The variable environmental conditions resulting from forest fragmentation in eastern North America may promote the invasion of exotic plants by allowing them to colonize ideal habitat at the edges of forest openings (Luken et al. 1997; Meekins and McCarthy 2001; Flory and Clay 2006). Conditions at forest edges that may enhance plant invasions include increased light availability, disturbance, and nutrient availability (Matlack 1993; Watkins et al. 2003; Johnston and Johnston 2004). Importantly, the ability of an exotic plant to invade and the impact of invasive plants on resident plant communities may change along the environmental gradient

from edges to forest interiors (Watkins et al. 2003).

Invasions of the grass *Microstegium vimineum* (Trin.) A. Camus (common names: Japanese stiltgrass, Nepalese browntop, Chinese packing grass, basketgrass, Mary's grass) are an increasing threat to eastern deciduous forests and a concern for natural areas managers. First documented in Tennessee in 1919 (Fairbrothers and Gray 1972), *Microstegium* is currently found in at least 22 states in eastern North America and is listed as a noxious weed in three states (USDA and NRCS 2005). *Microstegium* is an aggressive and highly shade tolerant C₄ annual grass that produces up to 1000 seeds per plant (Winter et al. 1982; Horton and Neufeld 1998; Tu 2000, Gibson et al. 2002). It quickly invades disturbed areas due to high seed production, and can colonize open areas during the growing season by producing lateral tillers (Cheplick 2006). Once it invades, *Microstegium* creates near monospecific stands that are highly resistant to recolonization by native species (Barden 1987). *Microstegium* commonly occurs in low-lying wet forests and riparian areas where its seed is dispersed by flowing water, animals, and human activities (Redman 1995; Tu 2000).

Microstegium can thrive under full sunlight conditions (Winter et al. 1982). However, it was found to be limited by light availability in the deeply shaded environment below stands of the clonal understory tree

Asimina triloba where light was reduced to approximately 1% of ambient sunlight (Cole and Weltzin 2005). Under moderate shade in ambient understory light conditions, *Microstegium* survival and growth is high (Cole and Weltzin 2005), likely because it has the ability to take advantage of sun flecks through rapid photosynthetic response (Horton and Neufeld 1998). At deciduous forest edges such as roadsides, stream banks, and along old logging roads and trails where *Microstegium* commonly invades (Barden 1987; Cole and Weltzin 2004), light availability decreases as distance from edges increases (Matlack 1993; Honnay et al. 2002). Under these conditions, the invasion potential of *Microstegium* may be limited by decreased light in the forest understory, which could reduce its impact on the resident plant community in forest interiors (Claridge and Franklin 2002). Alternatively, if shaded conditions do not produce light levels low enough to limit *Microstegium* in forest interiors, it may be able to invade deep into forests and negatively impact resident plants (Leicht et al. 2005).

The purpose of this study was to determine how experimental light treatments simulating the gradient of light availability from forest edges to forest interiors affect the growth of *Microstegium* and its impact on resident plant communities. The experiment was a common garden design where large pots containing resident plant communities were grown in an open field with or without *Microstegium* under three light treatments. The *Microstegium* seed stock used in the experiment was contaminated with *Dichanthelium clandestinum* (L.) seed (< 5%), a dominant native perennial grass (Mou et al. 2005) that commonly co-occurs with *Microstegium* (S.L. Flory, pers. observation). While this contamination was unexpected, it allowed for an assessment of the interaction between *Microstegium* and *Dichanthelium* across an important environmental gradient. Specifically, we addressed the following questions: (1) How do experimental light treatments affect the interaction between *Microstegium* and *Dichanthelium* and (2) Does invasion by *Microstegium* and *Dichanthelium* reduce resident community growth and are effects determined by light treatments?

Evaluation of these questions will be immediately useful for researchers and natural areas managers who are interested in predicting where *Microstegium* has the potential to invade, the impact of *Microstegium* on resident plant communities, and the outcome of competition between *Microstegium* and other grasses over an environmental gradient.

METHODS

Study site

Lilly-Dickey Woods (LDW), located approximately 6 km northeast of Nashville, Indiana (UTM zone 16 NAD-83; 0567375 m E, 4343237 m N), is a property of the Indiana University Research and Teaching Preserve (<http://www.indiana.edu/~preserve/>). It consists of 225 ha of old-growth and second-growth oak-beech-maple (*Quercus-Fagus-Acer*) eastern deciduous forest. The topography is elongated ridge tops and deep ravines with unglaciated thin stony silt loam soils derived from sandstone and shale (Rogers et al. 1946). LDW receives 102.10 cm of precipitation per year on average and has average daily maximum temperatures of 29.4 °C during the summer months (Noble et al. 1990). LDW is part of Brown County Hills, a 120,000 ha region that is the largest contiguous block of forest remaining in Indiana. *Microstegium vimineum* is invading LDW near a trail that runs along a ridge top through the southern portion of the preserve.

Resident community

At LDW, we observed that the most common resident species competing with invading *Microstegium* at the herbaceous level were the graminoids *Poa alsodes* (A. Gray), *Leersia virginica* (Willd.), *Carex radiata* (Wahlenb.), *Juncus tenuis* (Willd.), and *Elymus hystrix* (L.) (hereafter referred to only by genus). Taxonomy follows Gleason and Cronquist (1991). We collected individual tillers from established plants of *Poa*, *Leersia*, *Carex*, and *Juncus* from LDW and *Elymus* and *Setaria viridis* (L.) from the Indiana University Botany

Experimental Field (IUBEF) in Bloomington, Indiana on 26 May 2005. Three individual tillers of *Poa*, *Leersia*, *Carex*, *Juncus*, and either *Elymus* or *Setaria* were transplanted into 48.5 L (20 cm diameter, 15 cm deep) plastic pots filled with a 1:1 mix of sand and field soil collected from Monroe County, Indiana. Both *Setaria* and *Elymus* were not added to each pot due to problems in distinguishing between tillers of each species at the vegetative stage. Species identification of *Setaria* and *Elymus* was apparent at the end of the experiment when the plants were much larger. Few naturally occurring seeds germinated from the field-collected soil (and no *Microstegium*), so they were ignored in the analysis. Twenty-four additional pots were filled with the soil and sand mix and set aside to be planted later with *Microstegium* seed stock. Any tillers that had died within 10 days were replaced.

Light treatments

At LDW, we characterized the natural light environment where *Microstegium* was invading by establishing transects at the center and edge of the trail and parallel to the trail in interior forest. We measured photosynthetic photon flux density (PPFD, AccuPAR Linear PAR/LAI ceptometer, Decagon Devices, Inc., Pullman, Washington) at midday with no clouds at eight locations along each of the three transects. The values were then converted to percentage of full sunlight (Figure 1).

Two pots containing the resident community and one pot without vegetation were placed on each of 24 standard wood shipping pallets spaced 2.5 m apart in an open field at IUBEF. The pallets were placed in a 6 x 4 grid with the long side of the grid oriented north and south. One meter cube shade tents constructed of woven synthetic fabric (Lumite, Gainesville, Georgia) and 2.45 cm PVC piping were secured over eight randomly selected pallets to create the "part shade" treatment. The vertical posts of the frame were 1.1 m in length, such that there was a 10-cm gap below the tent to allow for airflow. The tents also had 10 cm x 25 cm openings cut in their north and east sides to increase airflow and allow

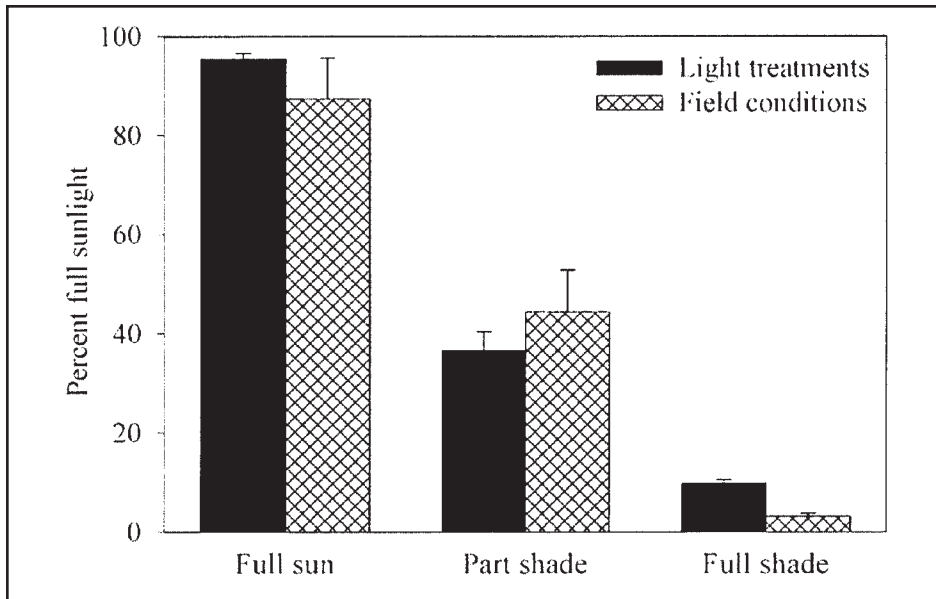


Figure 1. Percentage full sunlight under the three light treatments (mean \pm 1 SE; $n = 8$ per treatment) compared to along transects at the center and edge of a trail and parallel to the trail in interior forest at LDW ($n = 8$ measurements per transect). Full sun photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was 1005 at LDW and 1434 at IUBEF.

insects to enter. Eight additional pallets were selected to be covered with three tent layers to create the “full shade” treatment, and eight pallets received no tents for the “full sun” treatment. Light measurements were taken inside each tent after they had been erected (AccuPAR Linear PAR/LAI ceptometer, Decagon Devices, Inc., Pullman, Washington) and were comparable to the measurements along the trail at LDW (Figure 1). On 21 June 2005, 27 days after the resident communities were assembled, 0.67 g (mean \pm 1 SE; 540 ± 12.59 seeds) of *Microstegium* seed stock (collected November 2002, Raleigh, North Carolina) were added to one of the pots containing the resident community and the pot containing no vegetation on each pallet. One pot per pallet was left with only the resident community. Thus, the experiment was a completely randomized design with three community types across three light levels replicated eight times.

The pots were watered daily except during rain events and were treated with water soluble fertilizer with N-P-K ratio of 20:20:20 (Peters Professional, The Scotts Company, Marysville, Ohio) six and eight weeks after the *Microstegium* seed stock was added to the pots. Following seed germination, *Dichantheium* was growing

in the pots where seed had been added and not in the pots containing only the resident community, so it was clear that it was inadvertently introduced and had not accidentally colonized the pots. We determined that the *Microstegium* seed stock used in the experiment contained $4.5 \pm 0.4\%$ (mean \pm 1 SE) *Dichantheium*. On 23 September 2005, fourteen weeks after the *Microstegium* seed stock was added, and just prior to the *Microstegium* setting seed, aboveground biomass was harvested, sorted by species, dried to constant mass in a 65 °C oven, and weighed.

Statistical analyses

Fixed effects analysis of variance (SAS Institute 2002) was used to evaluate the effect of resident community treatment (*Microstegium* and *Dichantheium* grown alone or with resident community), light treatment, species identity, and their interactions on *Microstegium* and *Dichantheium* aboveground biomass. ANOVA was used to examine the effect of invasion treatment (invaded or uninvaded), light treatment, species identity, and all interactions on total resident community biomass. When the effect of species identity significantly interacted with the light or

invasion treatments, the same analysis was used to evaluate the responses of individual resident species.

Microstegium and *Dichantheium* data met the assumption of normality but had unequal variances, and resident community data did not meet either the assumption of normality or homogeneity of variances. Transformations did not correct these problems in either data set. Therefore, we applied distribution-free randomization tests (with 9999 iterations) for comparison with the results from ANOVA to evaluate the treatments (Edgington 1987; Manly 1991). A randomization test determines a *P*-value by comparing an observed test statistic to a distribution of the test statistic that is expected under the null hypothesis that the treatments have no effects. We created a randomization test equivalent of ANOVA by encompassing Proc GLM code within a SAS randomization macro program (Cassell 2002). We used the randomization test to estimate bias-corrected accelerated 95% confidence intervals around the treatment means (Efron and Tibshirani 1993). Confidence intervals around a treatment mean that do not overlap the mean of the second treatment indicate a significant difference between the two treatments at $P < 0.05$. All results from the randomization tests were equivalent to those obtained using ANOVA; therefore, we only report the ANOVA results here.

RESULTS

Microstegium and *Dichantheium*

Based on the invader seed mixture (95.5% *Microstegium*, 4.5% *Dichantheium*), we would expect the final biomass of pots containing the two invaders to be approximately 95% *Microstegium* and 5% *Dichantheium* under all light treatments. However, there were significant differences in invader responses to light treatments (Figure 2, Table 1). Despite its small proportion in the seed stock, *Dichantheium* produced over 22 times more biomass than *Microstegium* under the full sun treatment (Tukey post-hoc test $P < 0.0001$), and it produced approximately twice as much biomass as *Microstegium* under

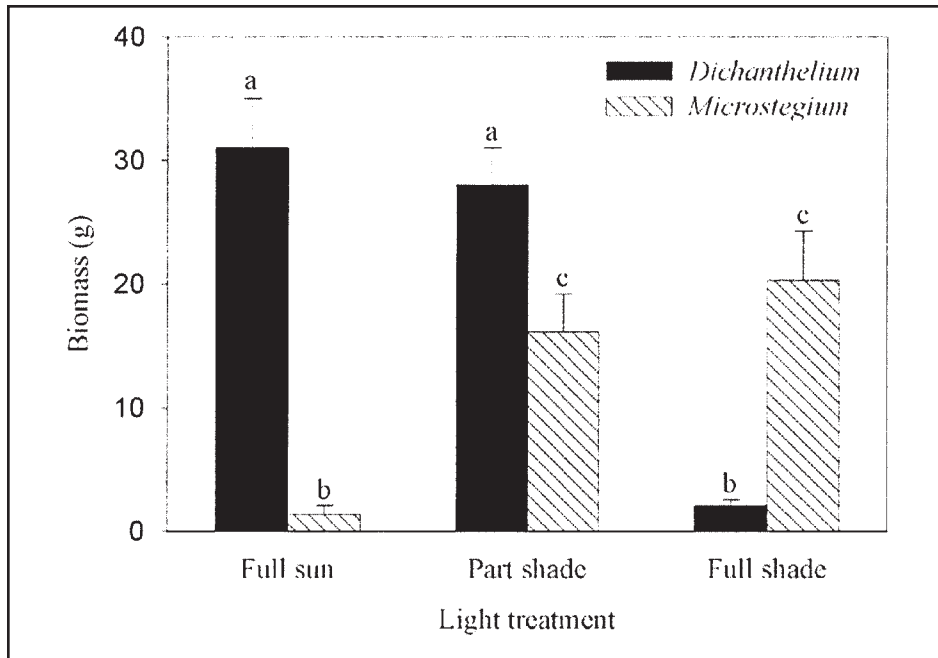


Figure 2. Effects of full sun, part shade, and full shade light treatments on aboveground biomass of *Dichanthelium* and *Microstegium* (least-squares means \pm 1 SE, n = 8 per treatment). Different letters indicate significant differences at $P < 0.05$.

the part shade treatment ($P < 0.0001$). In contrast, under the full shade treatment, *Microstegium* produced nearly 10 times greater biomass than *Dichanthelium* ($P < 0.0001$). Nevertheless, under the full shade treatment, *Dichanthelium* was still more productive than *Microstegium* on a per seed basis.

Resident community

There was a significant main effect of light on the resident community (Table 1) with the greatest productivity occurring under the part shade treatment (Figure 3). There was also a significant interaction between light and invasion treatment, such that *Microstegium* and *Dichanthelium* reduced overall resident community biomass under the part shade treatment but not under the full sun or full shade treatments (Figure 3, Table 1). Notably, the combined absolute productivity of *Microstegium* and *Dichanthelium* was greater in part shade (44.17 g) than in full sun (32.37 g) or full shade (23.0 g).

There was an interaction between species identity and invasion, indicating that resident community species varied in their responses to the invasion treatment (Figure 4, Tables 1, 2). Three of the six resident community species (*Leersia*, *Carex*, and *Juncus*) produced less biomass when invaded by *Microstegium* and *Dichanthelium*. *Setaria*, *Elymus*, and *Poa* also had lower productivity when invaded but the trends were not statistically significant. Further, resident species varied in their responses to the light treatments, with *Poa* producing the greatest biomass under full shade and *Setaria* producing the greatest biomass under full sun, with all other species having the greatest productivity under the part shade treatment (Figure 4, Tables 1, 2). There was a marginally significant ($P = 0.0502$) three-way interaction between species, invasion, and light (Figure 4, Table 2). For example, *Poa* and *Setaria*, unlike other species, produced more biomass when invaded versus uninvaded under full sun conditions, but less under part shade and full shade conditions (Figure 4).

Table 1. Results of ANOVA examining the fixed effects of species identity, resident community (grown alone or with the resident community), light treatment, and interactions on the biomass of *Microstegium* and *Dichanthelium* and the effects of species identity, invasion (grown alone or invaded), light treatment, and interactions on the biomass of the resident community.

<i>Microstegium</i> & <i>Dichanthelium</i>	Aboveground biomass		
	df	F	P
Species	1	38.14	<0.0001 ***
Resident community	1	50.78	<0.0001 ***
Light	2	25.01	<0.0001 ***
Species x resident community	1	4.42	0.0384 *
Species x light	2	133.55	<0.0001 ***
Resident community x light	2	0.93	0.3968
Species x resident community x light	2	13.66	<0.0001 ***
Resident Community			
Species	5	77.26	<0.0001 ***
Invasion	1	16.69	<0.0001 ***
Light	2	3.98	0.0201 *
Species x invasion	5	2.77	0.0189 *
Species x light	10	4.85	<0.0001 ***
Invasion x light	2	7.33	0.0008 **
Species x invasion x light	10	1.87	0.0502

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

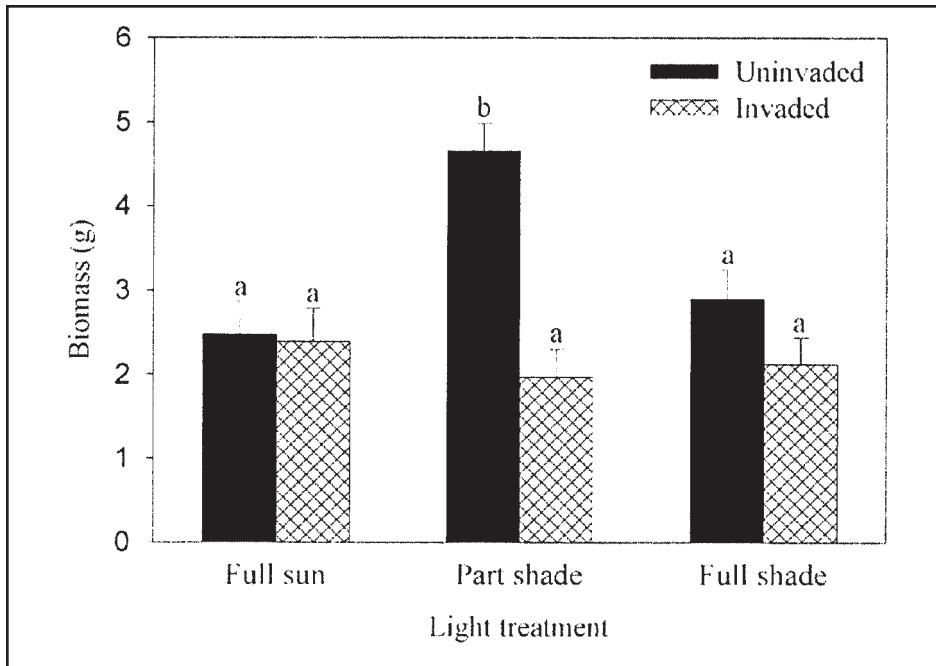


Figure 3. Effects of *Microstegium* and *Dichantheium* invasion on average resident community biomass under the three light treatments (least-squares means \pm 1 SE, n = 8 per treatment). Different letters indicate significant differences at $P < 0.05$.

DISCUSSION

How do experimental light treatments affect the interaction between *Microstegium* and *Dichantheium*?

The unexpected presence of *Dichantheium* seed in the *Microstegium* seed stock provided the opportunity to examine the interaction between a dominant native grass and invasive exotic grass across three experimental light treatments. The relative success of the two grasses was strongly affected by the light treatments, with *Dichantheium* dominating under full sun and *Microstegium* dominating in full shade. The two grasses produced more similar biomass under the part shade treatment. These results suggest that: (1) light environment can greatly affect the competitive balance between an exotic and a dominant native grass and (2) *Microstegium* may have greater success invading areas with lower light levels.

In addition to light, other environmental factors probably varied among the light treatments, which may have influenced invasion dynamics. For example, despite daily watering, it was observed that pots

under the full sun treatment often had much drier soils than pots in the part shade and full shade treatments. There was presumably also a difference in wind movement among the treatments, given that the part shade and full shade treatments were covered by one and three tent layers, respectively, while the full sun treatment was uncovered. Differences in air movement could have accounted for some of the differences in soil moisture loss. Despite the variations in light and air movement, no difference in air temperature was found among the treatments (data not shown). The dissimilarity in soil moisture among our treatments may have interacted with light availability to influence growth dynamics. Despite the inability of this experiment to clearly distinguish effects due to light, soil moisture, and other environmental variables, the results of this experiment are informative for predicting *Microstegium* invasion since these environmental variables also co-vary in nature and are highly correlated with distance to forest edges (Matlack 1993; Cadenasso et al. 1997; Honnay et al. 2002).

Microstegium utilizes the C_4 photosynthetic pathway (Winter et al. 1982), which is more efficient at conserving moisture than

the C_3 photosynthetic pathway employed by *Dichantheium* and most other native perennial grasses that occur in eastern deciduous forests (Bell and Quinn 1987; Ehleringer and Monson 1993; Yu et al. 2005). However, most accounts of *Microstegium* invasions are from moist riparian and lowland areas (Barden 1987; Redman 1995), suggesting that *Microstegium* is either not tolerant of dry conditions or limited by other factors, such as disturbance or seed dispersal. *Microstegium* is highly shade tolerant (Winter et al. 1982; Barden 1987; Horton and Neufeld 1998; Claridge and Franklin 2002), but is not inhibited by high light conditions under lab conditions (Horton and Neufeld 1998). This suggests that *Microstegium* could be invasive over a wider range of light conditions than those imposed by the experimental light treatments in this study if other environmental factors, such as soil moisture, are not strictly correlated with light availability. However, *Microstegium* is not likely to invade all forest habitats, such as those with high light availability, low soil moisture, and established populations of *Dichantheium*. Further, it is not known how successful *Microstegium* might have been in the full sun treatment if *Dichantheium* had not been present. If competition with *Dichantheium* helped to limit the success of *Microstegium* under the full sun treatment, then *Microstegium* may be invasive across a wider range of environmental conditions than these results indicate, given that *Dichantheium* may not be present at all of those sites. Further study is needed to determine the role of competition with resident plants and the influence of a broader range of environmental conditions, such as light availability and soil moisture, in limiting *Microstegium* invasions.

Does invasion of *Microstegium* and *Dichantheium* reduce resident community growth and are effects determined by light treatments?

In this study, the impact of *Microstegium* and *Dichantheium* invasion on the resident community varied with light treatments. Introduction of the two invaders significantly reduced resident plant growth under part

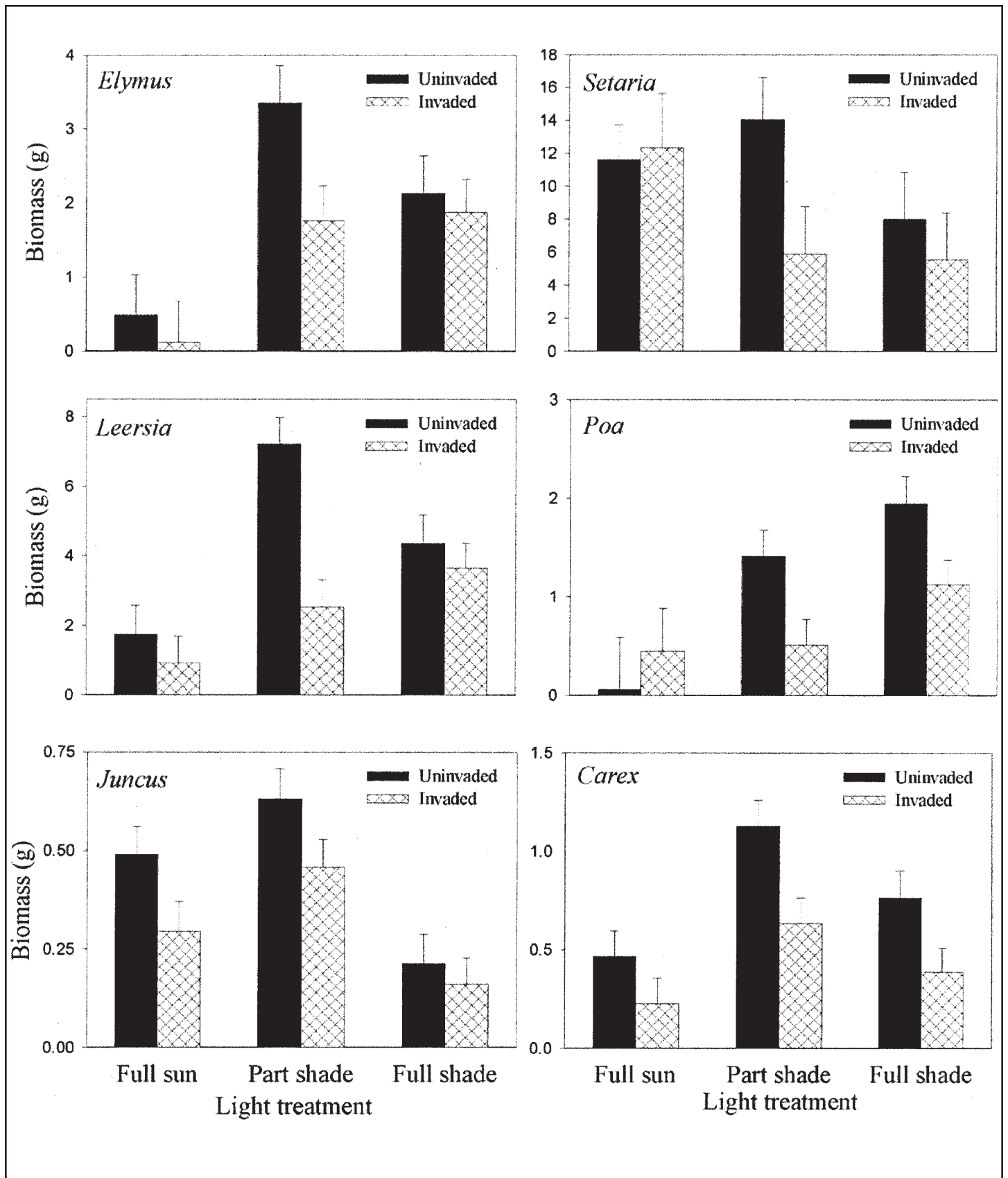


Figure 4. Effects of *Microstegium* and *Dichanthelium* invasion on the biomass of six individual resident community species under three light treatments (least-squares means \pm 1 SE). There is a three-way interaction between invasion treatment, light treatment, and resident community species as reported in Table 1. Note the differences in y-axis (biomass) scaling.

Table 2. Results of ANOVAs examining the effects of invasion (grown alone or invaded), light treatment, and invasion x light on the biomass of individual resident community species.

Resident community species	Aboveground biomass		
	df	F	P
<i>Setaria</i>			
Invasion	1	2.11	0.161
Light	2	1.73	0.2012
Invasion x light	2	1.35	0.282
<i>Leersia</i>			
Invasion	1	10.81	0.0021 **
Light	2	11.07	0.0001 ***
Invasion x light	2	4.45	0.0179 *
<i>Elymus</i>			
Invasion	1	3.12	0.0854
Light	2	9.85	0.0004 **
Invasion x light	2	1.13	0.3348
<i>Poa</i>			
Invasion	1	2.41	0.131
Light	2	6.03	0.0061 **
Invasion x light	2	1.47	0.2464
<i>Carex</i>			
Invasion	1	11.93	0.0013 **
Light	2	8.4	0.0009 **
Invasion x light	2	0.47	0.6284
<i>Juncus</i>			
Invasion	1	5.63	0.0225 *
Light	2	12.48	<0.0001 ***
Invasion x light	2	0.58	0.5649

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

shade conditions but not under the full sun or full shade treatments. Although this experiment could not distinguish between the relative contributions of *Microstegium* and *Dichanthelium* to the reduction in resident species biomass, a reasonable approximation is that the reduction in growth was a result of the proportion of the biomass of each species in each pot (Goldberg and Werner 1983). Therefore, in part-shade invaded resident community pots, where 36.5 % of the biomass was *Microstegium* and 63.5 % *Dichanthelium*, the majority of the reduction in growth of resident species

in the part-shade treatment was likely due to *Dichanthelium* invasion.

All resident community species exhibited reduced growth when invaded, although not all reductions were statistically significant. Notably, only *Setaria* is a C₄ annual species. The other five resident community species are C₃ perennial graminoids that characteristically grow more during cooler months and not during the summer months when this study was conducted (Ehleringer and Monson 1993). Therefore, the reduction in growth of resident species under invaded conditions might be even greater

if the experiment was allowed to progress through a full growing season, because the resident species would be impacted by invasion during the time when they are actively acquiring resources and accumulating biomass. In contrast, the impact of invasion may be reduced if resident species are more competitive with *Microstegium* during the cooler months, which could compensate for the negative effects of invasion that occur during summer months. Moreover, given the differences in responses of the resident species, effects of *Microstegium* invasion may vary with local community composition.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

In this study, the invasive success of *Microstegium*, in the presence of the dominant perennial grass *Dichanthelium*, was determined by our light treatments. *Microstegium* was dominant in full shade, *Dichanthelium* was dominant in full sun, and the two species were “more equal” in part shade. Invasions of the two grasses reduced resident plant community growth under the part shade treatment but not in full sun or full shade. Because *Microstegium* has the ability to invade large areas and produce abundant biomass and prolific numbers of seed, it has the potential to negatively impact the growth of native herbaceous species. This could lead to changes in herbaceous plant community composition in forests if invasions of *Microstegium* differentially reduce growth and survivorship among species. These and other changes to the native plant community could potentially affect a range of ecosystem processes (Kourtev et al. 1998; Ehrenfeld et al. 2001; Kourtev et al. 2002).

Given the range of environmental conditions where *Microstegium* might be invasive and the potential impact on resident plant communities, land managers should quickly remove *Microstegium* through chemical or mechanical means (Tu 2000; Judge et al. 2005). To restore invaded sites, re-treatment may be necessary to exhaust the seed bank; highly competitive native species, such as *Dichanthelium*, may need to be planted to resist future invasions.

However, if the goal of natural areas managers is to restore a high diversity herbaceous community, the presence of *Dichanthelium* could impede such goals.

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