

Variation for phenotypic plasticity among populations of an invasive exotic grass

Tyler Droste · S. Luke Flory · Keith Clay

Received: 7 May 2009 / Accepted: 21 September 2009 / Published online: 1 October 2009
© Springer Science+Business Media B.V. 2009

Abstract Phenotypic plasticity is a common feature of plant invaders, but little is known about variation in plasticity among invading populations. Variation in plasticity of ecologically important traits could facilitate the evolution of greater plasticity and invasiveness. We examined plasticity among invasive populations of *Microstegium vimineum* (Japanese stiltgrass), a widespread and often dominant grass of forests in the eastern U.S. with two separate experiments. First, we exposed seven *Microstegium* populations to a drought treatment in growth chambers and monitored growth and physiological responses. Then, we established a greenhouse experiment using a subset of the populations; two that exhibited the most divergent responses and one intermediate population. In the greenhouse, we manipulated drought and shade and evaluated biomass production and specific leaf area (SLA). *Microstegium* exhibited plasticity for biomass production and SLA in the greenhouse experiment, and populations significantly varied in the degree of plasticity under drought and shade treatments. Two populations significantly increased biomass production under favorable conditions, unlike the third population. The most productive populations also responded to shade stress via greater SLA, possibly allowing for

greater utilization of available light, while the third population did not. These results show that *Microstegium* can exhibit plastic responses to environmental conditions. Moreover, variation for plasticity among populations provides the potential for further evolution of plasticity. Future studies should focus on the relative importance of plasticity for the success of *Microstegium* and other plant invaders and evaluate post-introduction evolution of plasticity.

Keywords Drought · Japanese stiltgrass · *Microstegium vimineum* · Shade

Introduction

Exotic plant invasions can reduce native species diversity, alter ecosystem processes, and change the physical features of habitats (e.g., Mack et al. 2000). Much research focuses on predicting which introduced plants are likely to be invasive (Higgins et al. 1999; Kolar and Lodge 2001; Rejmanek 2000) and identifying habitats that are vulnerable to invasions (Whitcraft et al. 2007; Zedler and Black 2004). To recognize potential invaders and limit their impacts on native communities, we need to identify the characteristics that enhance invasiveness.

Phenotypic plasticity, the ability of a genotype to express different phenotypes under different

T. Droste · S. L. Flory (✉) · K. Clay
Department of Biology, Indiana University, 1001 East 3rd
Street, Bloomington, IN, 47405USA
e-mail: sflory@indiana.edu

environmental conditions (Pigliucci 2001; Schlichting 1986) has long been hypothesized to be a feature of successful plant invaders (Baker 1965). Plasticity for ecologically important traits may promote invasiveness by enhancing the ability to withstand adverse environmental conditions or to respond positively to favorable conditions. It is also possible that an invader could be both relatively tolerant of unfavorable conditions and flexible enough to increase productivity when more ideal conditions arise (Richards et al. 2006). Such plants would likely be invasive across the widest possible range of conditions. Phenotypic plasticity in invasive plants has only recently been investigated empirically (e.g., Bossdorf et al. 2008; Burns and Winn 2006; Claridge and Franklin 2002; Lavergne and Molofsky 2007; Maron et al. 2004; Muth and Pigliucci 2007). Studies across diverse taxa indicate that phenotypic plasticity may be a common trait of plant invaders (reviewed by Richards et al. 2006).

In addition to plasticity promoting invasiveness, variation for plasticity among introduced populations may allow an invader to evolve greater plasticity, resulting in colonization of more diverse habitats and plant communities (Agrawal 2001; Lavergne and Molofsky 2007; Maron et al. 2004; Richards et al. 2006). For example, gene flow among populations may alleviate genetic bottlenecks and increase genetic diversity, resulting in greater evolutionary potential for invading populations (Ellstrand and Schierenbeck 2000). Highly plastic populations may then persist during extreme environmental fluctuations or in unfavorable habitats. Variation for phenotypic plasticity among invading populations has rarely been documented (Lavergne and Molofsky 2007), but may be an important factor in explaining the invasiveness of exotic plants. To understand the mechanisms of invasiveness, identify habitats vulnerable to invasion, and determine the potential range expansion of exotic species, information on variation for phenotypic plasticity in invasive plant species is required.

In this study, we evaluated phenotypic plasticity and variation for plasticity among populations of *Microstegium vimineum* (Japanese stiltgrass), a shade-tolerant invasive annual grass. *Microstegium* was introduced to the USA from Asia in the early 1900s (Fairbrothers and Gray 1972; Winter et al. 1982) and is currently listed as invasive in 22 eastern

states (USDA and NRCS 2005). *Microstegium* is slow to invade undisturbed vegetation, but rapidly invades disturbed, mesic, shaded areas (Barden 1987) such as floodplains, lowland forests, wet meadows, streambanks, trails, roadsides, and forest openings (Cole and Weltzin 2004; Gibson et al. 2002; Redman 1995). Invasions can be limited by low soil moisture and deeply shaded conditions (Cole and Weltzin 2005; Flory 2009). *Microstegium* creates dense, nearly monospecific stands that reduce native plant diversity and productivity, inhibit forest regeneration, and threaten to alter forest species composition and successional trajectories (Flory and Clay 2009; Oswalt et al. 2007). Claridge and Franklin (2002) documented that plants from a single *Microstegium* population exhibited plasticity in biomass allocation and the production of reproductive structures, but studies evaluating variation for plasticity among invading populations are needed.

To assess the degree of variation for phenotypic plasticity among *Microstegium* populations, we evaluated the responses of seven populations to different environmental conditions. Variation for phenotypic plasticity exists when distinct populations vary in their plastic responses to the same range of environmental conditions. Here, we imposed drought and shade treatments using controlled growth chamber and greenhouse experiments and quantified *Microstegium* photosynthesis, water use efficiency, productivity, and SLA. We addressed two specific questions: (1) Does *Microstegium* exhibit plastic responses to drought and shade? (2) Is there variation for phenotypic plasticity among invasive populations?

Methods

Collection of populations

Between 16 May 2005 and 10 June 2005, we collected *Microstegium* seedlings from seven populations in southern Indiana (Table 1). To ensure that the seedlings we collected represented genetically distinct lines, we collected seedlings from extant populations separated by 1.5–108 km. At the time of collection, seedlings were newly germinated and were less than 5 cm tall.

Variation in the performance of plant progeny, and differences in an individual's phenotype, may be

Table 1 Counties, properties, sites, abbreviations, and locations of the seven populations of *Microstegium* used in the study

County	Property	Site	Abbreviations	Location
Clark	Clark State Forest	Logging site	CF	38°28'35" N 85°50'10" W
Monroe	Hoosier National Forest	Deam Wilderness	D	39°01'58" N 86°20'26" W
Brown	Lilly-Dickey Woods	Lookout Tower	LL	39°14'38" N 86°13'00" W
Brown	Lilly-Dickey Woods	Transect	LT	39°15'18" N 86°12'32" W
Monroe	Morgan-Monroe State Forest	Farr Road	FR	39°18'58" N 86°27'14" W
Brown	Yellowwood State Forest	Lanam Ridge Road	L	39°14'00" N 86°20'39" W
Brown	Yellowwood State Forest	T.C. Steele	TC	39°07'21" N 86°20'45" W

All sites were located in Indiana, USA

influenced by the environment in which its maternal parent was growing (i.e., maternal effects, Roach and Wulff 1987). To ensure all experimental plants were produced under the same conditions, we grew ten seedlings from each of the seven populations in a uniform environment in the Indiana University greenhouse for the 2005 growing season. *Microstegium* produces both chasmogamous (i.e., outcrossed) and cleistogamous (i.e., obligately selfed) seeds (Cheplick 2006). In late September 2005, we collected all cleistogamous seeds from each individual (i.e., family) reared in the common greenhouse environment. Family was used here as the level of replication for investigating variation in plasticity among populations. Differences in plasticity among families reflect the genetic variation within populations.

Growth chamber experiment

To determine if there was variation for phenotypic plasticity among the seven *Microstegium* populations, we conducted a growth chamber experiment that included a drought treatment. In February 2006, we randomly selected 15 seeds from each of ten parent plants from the seven populations grown in the greenhouse. We stratified the seeds at 5°C on small plastic plates (1034 Rodac Plate, 65 × 15 mm) each containing two moistened filter papers (Whatman 55 mm circle). After 1 month of stratification, the

seeds were placed in a 30°C growth chamber (Percival Scientific, Inc., Perry, Iowa) with 12 h of light. To determine if there was variation among the populations for germination success, we recorded the proportion of seeds from each parent plant that had germinated after 12 days. We then transplanted two seedlings from each of the ten parent plants per population into 5 cm × 5 cm cell packs containing Metro Mix 360 (Sun Gro Horticulture, Ltd., Bellevue, WA) and randomly positioned them in one of two identical growth chambers (Percival PCG-15, Percival Scientific, Inc., Perry, Iowa). After 1 month of growth, we transplanted the seedlings into 9 cm × 8.5 cm plastic pots containing Metro Mix and re-randomized their locations among the two growth chambers. Thus, each growth chamber had a random mix of control and drought-treated plants. The growth chambers were programmed for 12 h of light per day with daytime temperatures of 25.5°C and nighttime temperatures of 22°C. The light levels of the two growth chambers were very similar (AccuPAR Linear PAR/LAI ceptometer, Decagon Devices, Inc., Pullman, Washington; mean ± SE photosynthetic photon flux density (PPFD); mol m⁻² s⁻¹; 358 ± 4.1 vs. 368 ± 1.9). Growth chamber humidity was set to 80% during the day and 60% at night.

We watered all plants to saturation every other day for 10 days to allow the plants to establish in the pots. Then, one of the two plants per parent was randomly selected to receive a drought treatment while the other

served as a well-watered control. The drought treatment consisted of not watering the selected individuals for 1 week, while the controls were watered to saturation every other day. In order to enhance the drought treatment, we reduced the humidity level in both growth chambers to 40% for both day and night. These conditions are comparable to the summer droughts that occur relatively often in the invasive range of *Microstegium*. We chose to focus on how drought affects seedling growth rather than seed germination because droughts rarely occur in our area in the spring when seeds are germinating but are relatively common in mid to late summer when seedlings are growing (NOAA and NCDC 2008).

After 1 week of drought, we measured the photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) for each individual using an infrared gas analyzer (LI-6400, LI-COR, Inc., Lincoln, Nebraska). We calculated instantaneous water use efficiency (WUE) for each plant by dividing photosynthetic rate by transpiration rate ($\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$). The aboveground biomass of each plant was harvested and dried at 65°C for 72 h and weighed (± 0.01 g). It has been suggested that in studies of phenotypic plasticity, performance should be measured by plant fitness (i.e., reproduction, Richards et al. 2006). Here we used total biomass production as a proxy for fitness since *Microstegium* biomass is highly correlated with seed production ($r^2 = 0.59$, $n = 40$; A. Shelton et al., unpublished data).

We analyzed the proportion of seeds germinated from each individual for the seven populations using analysis of variance (Proc GLM, SAS Institute Inc. 2002). We analyzed photosynthetic rate, WUE, and biomass using separate ANOVAs with the drought treatment as a fixed effect and population as a random effect. We did not include block as a factor in the model because the plants were completely randomized among treatments and growth chambers. With this design, phenotypic plasticity is confirmed when there is a statistically significant effect of treatment. Variation for plasticity is demonstrated by a significant treatment by population interaction following Valladares et al. (2006).

Greenhouse experiment

The results from the growth chamber experiment suggested that some populations varied in phenotypic

plasticity. Therefore, to test whether populations varied in plasticity, we conducted a second experiment in the greenhouse using the two most divergent and one average population (TC, CF, and LT) from the growth chamber experiment in terms of average photosynthetic rate, germination rate, and WUE. For example, CF had trends for greater biomass under no-drought conditions and greater WUE under drought conditions. In contrast, LT exhibited trends for reduced growth under no-drought conditions and greater WUE with no drought. By selecting extremes among the populations, we were better able to detect variation for plasticity, analogous to using divergent lines in a selection experiment to evaluate a trait of interest (Conner 2003).

We grew 96 *Microstegium* plants from the same seed lots used in the growth chamber experiment by first germinating cleistogamous seeds from each of eight parents from the TC, CF, and LT populations following the same method used in the growth chamber experiment. Then, four seedlings per parent were initially planted into cell packs to establish and then, after 2 weeks, were transplanted into 12.7 cm diameter clay pots containing Metro Mix. Five ml of Osmocote 14-14-14 fertilizer (The Scotts Company, Marysville, OH) was added to the pots and the plants were grown in the greenhouse with 12 h of artificial lighting for 20 days.

Drought and shade were manipulated in the greenhouse experiment because they are thought to be key determinants of *Microstegium* distribution (Cole and Weltzin 2004; Redman 1995) and dominance (Flory et al. 2007). We randomly assigned 96 plants ($4 \text{ plants} \times 8 \text{ parents} \times 3 \text{ populations} = 96 \text{ total plants}$) to one of the following four treatments: (1) shade and drought (S+/D+), (2) shade only (S+/D−), (3) drought only (S−/D+), or (4) no shade, no drought (S−/D−). Thus, the experiment was a 2×2 factorial design with two levels each of the shade and drought treatments. The shade treatment consisted of eight one-meter square shade tents (55 cm in height), constructed of two layers of woven synthetic fabric (Lumite, Gainesville, George) stretched over PVC piping. A 10 cm gap was left below the tents to allow for air flow. The shade treatment reduced ambient light availability by an average of $83 \pm 11\%$ (mean PPFD $\pm$ SE, ambient light 1172 ± 54 ; shade treatment 202 ± 12). The drought treatment was conducted by monitoring soil moisture daily and

allowing moisture levels to drop to 5% Volumetric water content (VWC; ECH₂O, EC-5 sensor, Decagon Devices, Inc., Pullman, WA, USA) before watering to saturation. Plants that did not receive the drought treatment were watered daily to saturation.

We separated the plants into one group receiving the shade treatment and a second group in full sun, and randomly assigned each plant to a location within one of the eight shade or full sun treatments. We arranged the groups of six plants within the shade or full sun treatments in a checkerboard pattern on the greenhouse benches. All plants were fertilized with 100 ml of a diluted Peter's 20-20-20 fertilizer (The Scotts Company, Marysville, OH) once per week during the course of the experiment.

After the plants had grown for 1 month under the treatments, up to 30 leaves were collected from each plant and the aboveground biomass was harvested, dried at 55°C to constant mass, and weighed (± 0.01 g). The biomass of the 30 harvested leaves was added to the whole plant biomass for final analysis. SLA a key trait for determining plant invasiveness (Grotkopp and Rejmanek 2007), was calculated by dividing the leaf area of the collected leaves (LI-3100 area meter, LI-COR, Inc., Lincoln, Nebraska) by the dry mass of those leaves (cm²/g). High SLA allows for increased light utilization in shaded environments and has been linked with elevated relative growth rates and invasion success (Grotkopp and Rejmanek 2007; Hamilton et al. 2005; Lake and Leishman 2004).

We analyzed the fixed effects of drought, shade, and population and their interactions on the biomass and SLA of the plants using analysis of variance (SAS Institute Inc. 2002). Inadvertently, the specific block locations of each plant were not recorded so block was not included in the model. We used the same criteria as in the growth chamber experiment to evaluate plasticity and variation for plasticity.

Results

Growth chamber experiment

Selfed lines derived from the seven populations of *Microstegium* exhibited variation for germination success of seeds produced in a common greenhouse environment ($F_{6,63} = 3.74$, $P = 0.003$; Fig. 1).

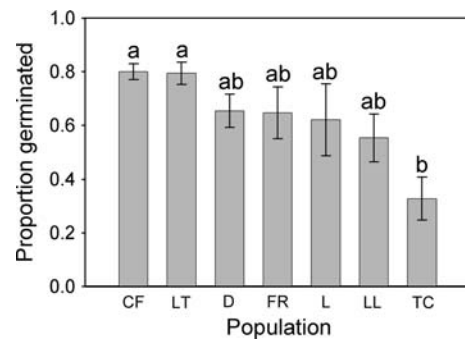


Fig. 1 Proportion of seeds germinated for seven populations of *Microstegium* (means $\pm$ 1 SE, $n = 15$ per population). Different letters indicate significant differences at $P < 0.05$

Populations CF and LT had the highest rate of germination (mean $\pm$ SE proportion germinated; 0.80 ± 0.03), which were 59% greater than TC, the population with the lowest rate of germination (0.32 ± 0.08). All other populations (LL, D, FR, L) were intermediate and did not differ in germination rates ($P > 0.05$; Fig. 1).

Despite differences in germination success, there were no overall differences among the seven *Microstegium* populations in the growth chamber in biomass production ($F_{6,6} = 0.97$, $P = 0.51$, Fig. 2a), photosynthesis ($F_{6,6} = 0.77$, $P = 0.62$, Fig. 2b), or WUE ($F_{6,6} = 1.21$, $P = 0.41$, Fig. 2c). The drought treatment did not affect biomass production ($F_{1,6.49} = 1.67$, $P = 0.24$), photosynthesis ($F_{1,6.79} = 0.01$, $P = 0.93$), or WUE ($F_{1,6.84} = 0.11$, $P = 0.75$). Similarly, there were no overall differences among the seven *Microstegium* populations in their response to the drought treatment (population $\times$ responses; interactions all $P > 0.05$).

Greenhouse experiment

Three *Microstegium* populations were specifically evaluated in the greenhouse experiment. Populations CF and LT exhibited significant plastic responses to the shade and drought treatments, but population TC did not, indicating variation for phenotypic plasticity among these populations. Overall, there were differences among the populations in biomass production such that population CF produced 26% greater biomass than LT and 61% greater biomass than TC (Table 2, Fig. 3a). The three populations did not differ in productivity under the limiting S+/D+

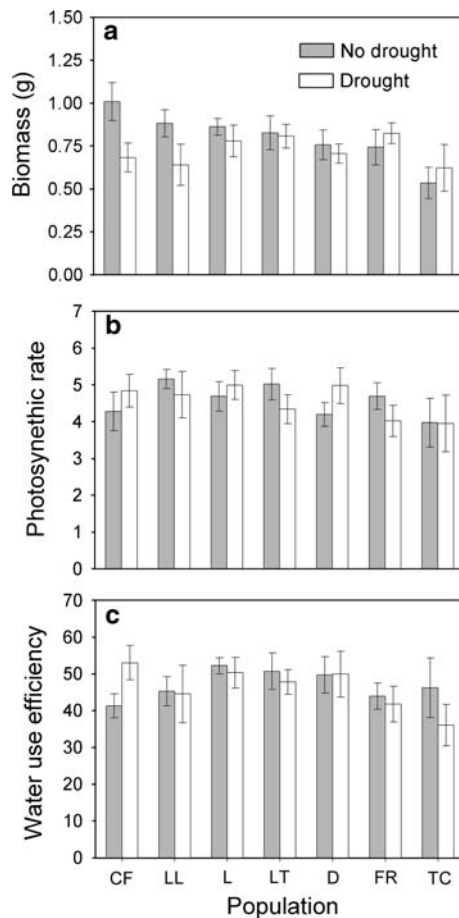


Fig. 2 Effects of the drought treatment in the growth chamber experiment on **a** plant biomass (g), **b** photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and **c** water use efficiency (WUE, $\mu\text{mol CO}_2 / \text{mmol H}_2\text{O}$) for seven *Microstegium* populations (mean $\pm$ 1 SE, $n = 10$ per population)

treatment (Fig. 3a). However, under the more favorable treatments (i.e., S+/D–, S–/D+, S–/D–), populations CF and LT exhibited plastic responses and were increasingly more productive, unlike TC which did not produce more biomass under more favorable conditions. CF and LT were consistently more productive than TC (Fig. 3b).

Overall, populations CF and LT had greater SLA than TC. In addition, populations CF and LT exhibited significant plastic SLA responses to the shade treatment while population TC did not (Fig. 3c, d). Populations CF and LT had similar SLA values for all treatments with significantly higher SLA values under shaded conditions (up to 31%). In contrast, SLA of population TC did not differ based on light availability (Table 2, Fig. 3c, d). The shade treatment induced stronger responses in SLA than the drought treatment, and there was a strong population $\times$ drought interaction for SLA (Table 2). The SLA of populations CF and LT were unaffected by the drought treatment but TC had lower SLA under S+/D– than S+/D+ (Fig. 3c, d).

Discussion

Plant invasiveness is determined in part by the ability of a species to succeed in a broad array of habitats. Species that exhibit phenotypic plasticity may expand their range by expressing adaptive phenotypes across varying environmental conditions (Pigliucci 2001). Further, variation for plasticity among invading

Table 2 Effects of population, shade, drought, and their interactions on the biomass and specific leaf area (SLA) of *Microstegium* in the greenhouse experiment

Effect	df	Biomass		SLA	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Population	2	25.57	<0.0001	28.56	<0.0001
Shade	1	28.24	<0.0001	37.78	0.008
Drought	1	7.34	0.008	2.79	0.10
Population $\times$ Shade	2	4.87	0.01	4.78	0.01
Population $\times$ Drought	2	3.66	0.03	5.14	<0.0001
Shade $\times$ Drought	1	0.66	0.42	0.37	0.54
Population $\times$ Shade $\times$ Drought	2	0.31	0.73	1.86	0.16

Note: *P* values listed in bold indicate significant differences at $P < 0.05$

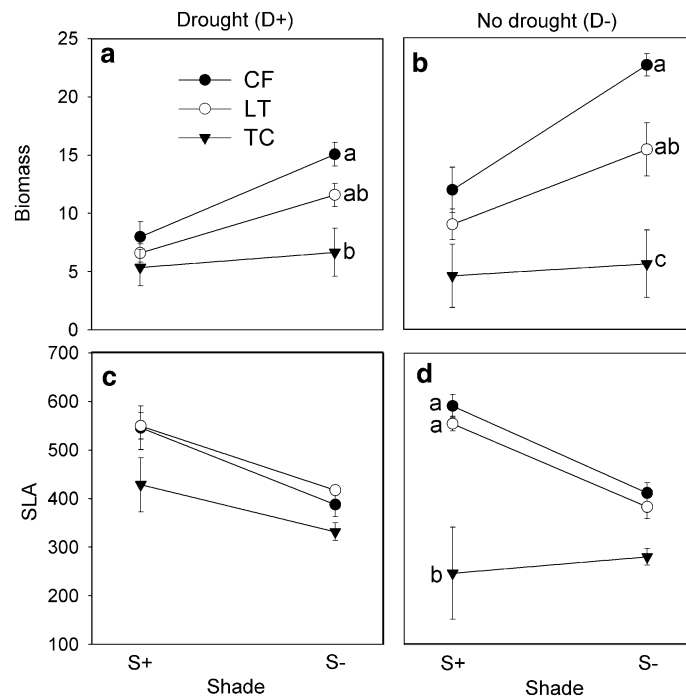


Fig. 3 Effects of the shade (S+/S-) and drought (D+/D-) treatments in the greenhouse experiment on **a, b** aboveground biomass (g) and **c, d** specific leaf area (SLA, cm²/g) of *Microstegium* populations CF, LT, and TC (mean $\pm$ 1 SE, n = 8 per population). Different letters among populations within treatments indicate significant differences at $P < 0.05$. No letters indicates no significant difference

populations may allow species to evolve greater invasiveness (Leger and Rice 2003; Richards et al. 2006). Our results demonstrate phenotypic plasticity in a widespread invasive grass for increased biomass production under more favorable conditions and greater SLA under stressful shaded conditions, two common traits of invasive species (Grotkopp and Rejmanek 2007; Leishman et al. 2007; Zou et al. 2007). Furthermore, there was variation in plasticity among the three selected populations.

After controlling for maternal effects, we found significant differences in plasticity among the invasive populations in the greenhouse experiment. Thus, *Microstegium* either did not experience a genetic 'bottle-neck' during introduction, repeated introductions ameliorated the bottleneck, or there has been rapid divergent evolution of *Microstegium*. The seven populations evaluated in the growth chamber experiment varied in germination rates, suggesting inherent variation in fitness among the populations, but there was no overall difference among populations in plasticity for productivity, photosynthesis, or WUE. However, when two divergent and one intermediate

population were evaluated in the greenhouse experiment where a wider range of environmental conditions were evaluated, they varied in their responses to those conditions. Given that we collected populations over a relatively small geographic area (three counties in south-central Indiana), the observed variation in germination, physiology, and biomass production among populations is likely a conservative measure of extant variation across the species range. The widespread distribution of *Microstegium* invasions in Indiana over a relatively short time period (~15 years), together with our results, suggests that there were likely multiple introduction events, which is common for invasive plants (Bossdorf et al. 2005).

We observed plasticity for biomass production and SLA, and differences in plasticity among populations. In the first growth chamber experiment, the drought treatment did not elicit a significant plastic response, although there was some evidence for differences in plasticity among populations. For example, average biomass production of populations CF and LT was greater under more favorable no-drought conditions. In addition, WUE of population CF increased under

population were evaluated in the greenhouse experiment where a wider range of environmental conditions were evaluated, they varied in their responses to those conditions. Given that we collected populations over a relatively small geographic area (three counties in south-central Indiana), the observed variation in germination, physiology, and biomass production among populations is likely a conservative measure of extant variation across the species range. The widespread distribution of *Microstegium* invasions in Indiana over a relatively short time period (~15 years), together with our results, suggests that there were likely multiple introduction events, which is common for invasive plants (Bossdorf et al. 2005).

drought stress, allowing those plants to conserve water, while WUE of population TC decreased with drought. When the data from the initial growth chamber experiment were subsequently analyzed with only the three populations used in the greenhouse experiment, there was a significant population $\times$ treatment interaction for biomass production.

Evaluation of the reduced set of populations in the greenhouse experiment provided clear evidence for plasticity and variation for plasticity among the populations. Two populations exhibited greater SLA under more stressful shaded conditions, allowing those plants to capture more light and grow more vigorously (Feng et al. 2007), but a third population showed no response. Plasticity for SLA has been widely documented as a key feature of plant invaders (e.g., Grotkopp and Rejmanek 2007; Leishman et al. 2007). Two of the three populations also responded to greater light and moisture by increasing biomass production, which is highly correlated with reproductive capacity in *Microstegium* and many other plant species. The two populations that exhibited increased SLA under shaded conditions (CF and LT) were both also more productive under more favorable no-shade, no-drought conditions. The significant effect of population in the greenhouse experiment may reflect the fact that we used two divergent and one intermediate population from the growth chamber experiment. However, the drought treatment in the greenhouse was more severe than in the growth chambers and was conducted for the entire length of the experiment instead of only in the last week as in the growth chamber experiment. Claridge and Franklin (2002) observed that *Microstegium* exhibited plasticity for biomass allocation and the production of reproductive structures when exposed to different nutrient and light levels. We showed that *Microstegium* exhibits phenotypic plasticity to a combination of different environmental conditions, but more importantly, we demonstrated that invasive populations may vary in plasticity.

The observed variation for phenotypic plasticity among *Microstegium* populations suggests that this invader has the potential to evolve greater vigor and opportunism (Richards et al. 2006). Evolution of increased vigor under environmental stress (e.g., greater cold hardiness, resistance to herbicides, or greater drought tolerance) may promote invasions in habitats that were previously too adverse. In addition,

more vigorous populations may grow at higher densities in invaded areas, causing additional declines in native community diversity and productivity. With predicted global climate changes in temperature, water availability, and disturbance regimes in eastern deciduous forests (McNulty and Aber 2001), our results suggest that the plasticity of *Microstegium* and its potential to evolve greater plasticity, may enable it to tolerate and adapt to changing conditions (Nussey et al. 2005). Thus, management efforts should focus on reducing the production and spread of propagules from established populations and the rapid identification and control of new invasions.

This study provides an important initial step in understanding how plasticity and variation for plasticity among populations promotes plant invasions. To further determine the role of plasticity in invasions, future studies should focus on the relationship between plasticity and invasiveness and on comparing the plasticity of invaders to the plasticity of native plants (Richards et al. 2006; van Kleunen and Fischer 2008). Studies should also be conducted using populations collected from a wider geographic area, ideally from across the invasive range. Evolution of increased plasticity following exotic plant introductions could be evaluated by comparing invasive populations to populations in the native range and the oldest parts of the introduced range (Muth and Pigliucci 2007). Post-introduction evolution of invasive plants may explain the lag time that often occurs between the initial introduction of non-native plants such as *Microstegium* and their recognition as invasive species (Crooks 2005).

Conclusions

Our results demonstrate that plasticity in an invasive grass promotes better performance across varying environmental conditions. More importantly, our results show variation for plasticity among invading populations, suggesting that some populations may be more invasive than others and may spread more rapidly from sites of introduction. Furthermore, variation for phenotypic plasticity among populations indicates there is the potential for evolution towards greater plasticity in *Microstegium*, and possibly enhanced invasiveness. Such adaptations could promote invasions in previously unfavorable habitats and result in further range expansion. Given these results,

management should focus on preventing the spread of seeds (i.e., gene flow) among populations to help prevent evolution of greater plasticity. More generally, our results provide evidence that plant invaders exhibit plasticity, and variation for plasticity, and call for additional studies to evaluate the post-introduction evolution of plasticity in exotic species.

Acknowledgments We thank Jennifer Rudgers, Lynda Delph, Heather Reynolds, Susan Cook, David Civitello, and Angie Shelton whose comments greatly improved the manuscript. We also thank Chris Herlihy who provided logistical support and advice on data collection and interpretation. Financial support was provided by the USDA Forest Service Hoosier National Forest, The Nature Conservancy, and the Howard Hughes Medical Institute.

References

- Agrawal AA (2001) Ecology—phenotypic plasticity in the interactions and evolution of species. *Science* 294:321–326
- Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL (eds) *The genetics of colonizing species*. Academic Press, New York, p 588
- Barden LS (1987) Invasion of *Microstegium vimineum* (Poaceae), an exotic, annual, shade-tolerant, C-4 grass, into a North Carolina floodplain. *Am Midland Nat* 118:40–45
- Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144:1–11
- Bossdorf O, Lipowsky A, Prati D (2008) Selection of pre-adapted populations allowed *Senecio inaequidens* to invade Central Europe. *Divers Distrib* 14:676–685
- Burns JH, Winn AA (2006) A comparison of plastic responses to competition by invasive and non-invasive congeners in the *Commelinaceae*. *Biol Invasions* 8:797–807
- Cheplick GP (2006) A modular approach to biomass allocation in an invasive annual (*Microstegium vimineum*; Poaceae). *Am J Botany* 93:539–545
- Claridge K, Franklin SB (2002) Compensation and plasticity in an invasive plant species. *Biol Invasions* 4:339–347
- Cole PG, Weltzin JF (2004) Environmental correlates of the distribution and abundance of *Microstegium vimineum*, in east Tennessee. *Southeastern 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
- Conner JK (2003) Artificial selection: a powerful tool for ecologists. *Ecology* 84:1650–1660
- Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience* 12:316–329
- Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc Natl Acad Sci USA* 97:7043–7050
- Fairbrothers DE, Gray JR (1972) *Microstegium vimineum* (Trin.) A. Camus (Gramineae) in the United States. *J Torrey Bot Soc* 99:97–100
- Feng YL, Wang JF, Sang WG (2007) Biomass allocation, morphology and photosynthesis of invasive and non-invasive exotic species grown at four irradiance levels. *Acta Oecol* 31:40–47
- Flory SL (2009) Management of *Microstegium vimineum* invasions and recovery of resident plant communities. *Restor Ecol* (in press)
- Flory SL, Clay K (2009) Invasive plant removal method determines native plant community responses. *J Appl Ecol* 46:434–442
- Flory SL, Rudgers JA, Clay K (2007) Experimental light treatments affect invasion success and the impact of *Microstegium vimineum* on the resident community. *Nat Areas J* 27:124–132
- 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
- Grotkopp E, Rejmanek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *Am J Bot* 94:526–532
- Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. *Ecol Lett* 8:1066–1074
- Higgins SI, Richardson DM, Cowling RM, Trinder-Smith TH (1999) Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conserv Biol* 13:303–313
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16:199–204
- Lake JC, Leishman MR (2004) Invasion success of exotic in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biol Conserv* 117:215–226
- Lavergne S, Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc Natl Acad Sci USA* 104:3883–3888
- Leger EA, Rice KJ (2003) Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecol Lett* 6:257–264
- Leishman MR, Haslehurst T, Ares A, Baruch Z (2007) Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytol* 176:635–643
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Maron JL, Vila M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecol Monogr* 74:261–280
- McNulty SG, Aber JD (2001) US national climate change assessment on forest ecosystems: an introduction. *Bio-science* 51:720–722
- Muth NZ, Pigliucci M (2007) Implementation of a novel framework for assessing species plasticity in biological invasions: responses of *Centaurea* and *Crepis* to phosphorus and water availability. *J Ecol* 95:1001–1013

- NOAA and NCDC (2008) National Oceanic and Atmospheric Administration, National Climate Data Center. <http://www.ncdc.noaa.gov/oa/ncdc.html>
- Nussey DH, Postma E, Gienapp P, Visser ME (2005) Selection on heritable phenotypic plasticity in a wild bird population. *Science* 310:304–306
- 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
- Pigliucci M (2001) Phenotypic plasticity: beyond nature and nurture. The Johns Hopkins University Press, Baltimore
- 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
- Rejmanek M (2000) Invasive plants: approaches and predictions. *Aust Ecol* 25:497–506
- Richards CL, Bosssdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecol Lett* 9: 981–993
- Roach DA, Wulff RD (1987) Maternal effects in plants. *Annu Rev Ecol Syst* 18:209–235
- SAS Institute Inc (2002) Cary, NC, USA
- Schlichting CD (1986) The evolution of phenotypic plasticity in plants. *Annu Rev Ecol Syst* 17:667–693
- USDA and NRCS (2005) The PLANTS Database. Data compiled from various sources by Mark W. Skinner. Version 3.5. National Plant Data Center, Baton Rouge, LA 70874-4490 USA
- Valladares F, Sanchez-Gomez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *J Ecol* 94:1103–1116
- van Kleunen M, Fischer M (2008) Adaptive rather than non-adaptive evolution of *Mimulus guttatus* in its invasive range. *Basic Appl Ecol* 9:213–223
- Whitcraft CR, Talley DM, Crooks JA, Boland J, Gaskin J (2007) Invasion of tamarisk (*Tamarix* spp.) in a southern California salt marsh. *Biol Invasions* 9:875–879
- Winter K, Schmitt MR, Edwards GE (1982) *Microstegium vimineum*, a shade-adapted C-4 grass. *Plant Sci Lett* 24:311–318
- Zedler PH, Black C (2004). Exotic plant invasions in an endemic-rich habitat: the spread of an introduced Australian grass, *Agrostis avenacea* J. F. Gmel., in California vernal pools. *Aust Ecol* 29:537–546
- Zou J, Rogers WE, Siemann E (2007) Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. *Funct Ecol* 21:721–730