Biological Invasions **4:** 339–347, 2002.

Compensation and plasticity in an invasive plant species

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Received 3 July 2000; accepted in revised form 20 August 2002

Key words: compensation, life history, *Microstegium vimineum*, nutrients, resource allocation plasticity, shading

Abstract

Plant plasticity under varying resources is one character that contributes to competitiveness and invasibility. The plasticity of plant modules of the invasive Japanese stilt grass (*Microstegium vimineum*) was examined under different light and nutrient levels using a balanced field and greenhouse study. Ample light and nutrients resulted in the greatest biomass accumulation in all plant modules. However, *M. vimineum* showed extreme plasticity, producing stolons and flowers (reproductive structures) under a wide range of environmental conditions except infertile, low light. The addition of nutrients under various shading regimes compensated for lower light levels, rendering little change in the allocation of carbon to reproductive structures. Data from the field study corroborate the greenhouse results, but also suggest plasticity in response to competition.

Introduction

Plastic resource allocation of plants in response to varying growing conditions affects dispersal, distribution, resilience, and speciation (Harper and Ogden 1970; Hickman 1975; Reekei and Bazzaz 1987a, b; Dong and de Kroon 1994), and hence plant's competitiveness (Berendse and Elberse 1990). Exotic invasives (non-indigenous species that invade and affect community structure and function) often are physiologically plastic allowing them to take advantage of a variety of habitats (Baker 1974; Luken et al. 1997; Meekins and McCarthy 2001). Species plasticity has been suggested as one character for predicting invasiveness (Rejmánek and Richardson 1996). However, we have little information on how the plasticity of exotic species may modify allocation of varying resources in time and space. Likewise, we do not know if resource allocation facilitates invasibility.

Exotic plants have been shown to modify resource allocation through changes in their morphology (Meekins and McCarthy 2001) and their physiology (Horton and Neufeld 1998). By changing leaf area or photosynthesis rate individuals maximize growth and reproduction under a variety of environmental conditions. Another potential factor influencing plasticity is the ability to compensate for a limiting environmental resource (Billings 1952). Studies have shown that fertilization increases plant photosynthesis and water-use efficiency (Tjoelker and Luxmoore 1991) and leaf area (Green and Mitchell 1992). Indeed, increased nutrients have been associated with decreased drought stress (Grime and Curtis 1976; Wray and Strain 1986). Theoretically, compensation of one resource for another would increase apparent plant plasticity, and thus increase competitive and invasive potential.

We measured one aspect of the plasticity of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus, by examining resource (biomass) allocation under various combinations of shade and nutrients. *M. vimineum* is a non-indigenous, invasive annual species that has become naturalized in many habitats in the eastern and southeastern United States (Redman 1995), and thus serves as a model organism for the study of plasticity in invasive exotics. *M. vimineum* is an annual C_4 grass uniquely adapted to growing in shade (Winter et al. 1992; Horton and Neufeld 1998) and in a variety of habitats (Barden 1987; Hunt and Zaremba 1992;

Redman 1995). It is a clonal species that spreads by stolons which root at the nodes creating new plants. Plasticity in morphology and resource allocation has been shown in numerous clonal plants forming ‘spacers’ such as stolons or rhizomes (de Kroon and Schieving 1991). Stoloniferous species in general have been found to produce long stolons under low light levels and/or limited nutrient availability (Dong and de Kroon 1994; Slade and Hutchings 1987) to ‘forage’ for better microenvironments (Cain 1994).

We were interested in two questions. How do invasive exotics modify resource allocation in the presence of various levels of resources in time and space, and does resource allocation plasticity facilitate the ability to succeed as an invader? We tested the hypothesis that *M. vimineum* increases stolon biomass or vegetative mass (stem elongation or rooting at the nodes) to increase spread in low light rather than expending energy on sexual reproduction. In addition, we hypothesized that the spread of *M. vimineum* under forest canopies was linked to the compensatory effects of abundant nutrients in light-stressed conditions.

Materials and methods

Greenhouse study

The greenhouse study consisted of 1200 juvenile *M. vimineum* plants transplanted from Meeman Biological Station (near Memphis, Tennessee), near the end of May 1999. Transplants were taken from a variety of locations. Five plants were planted in each of 240 15.24-cm wide azalea pots with saucers and randomly placed in the greenhouse. The environmental conditions were as follows ($n = 40$): (1) full sun, not fertilized, (2) full sun, fertilized, (3) 18–22% full sun, not fertilized, (4) 18–22% full sun, fertilized, (5) 2–7% full sun, not fertilized, and (6) 2–7% full sun, fertilized. The plants in the 2–7% full sun, fertilized treatment, mimicked the nutrient rich, low light floodplain forest habitat that *M. vimineum* tends to invade (Redman 1995).

The soil used was a nursery bulk mixture of three equal parts of nutrient poor topsoil, sand, and pine mulch. All treatments received an initial application of Peters Professional All Purpose Plant Food (1 teaspoon/gallon water 20-20-20 plus micronutrients; Spectrum Group, Division of United Industries Corporation, St. Louis, Missouri) to equalize starting soil nutrient and water conditions. Thereafter, all plants were watered as needed, with plants in the fertilized treatment receiving Peter’s every 10 days beginning with the first day of the experiment. Shaded plants were placed under upside-down tomato cages wrapped in shade cloth (100% nylon, 2.0 oz., Green 106, Type II, Tananbaum Textile Co., New York) once or twice to achieve the desired sunlight percentage. A LI-190SA Quantum Sensor was used to measure photosynthetic active radiation (PAR) to determine the amount of shade cloth to use. The greenhouse temperature varied from 19.9 °C to 34.9 °C.

Ten pots (50 plants) were harvested from each treatment and the control: (1) after 48 days of growth, (2) after 50% of the plants were flowering – [day 117], (3) 21 days after the second harvest – [day 138], and (4) 21 days after 50% of plants set seed – [day 158]. The plants were separated into plant modules (i.e., leaves, stems, stolons, roots, and flowers if present), and dried at 60 °C for 48 h and weighed to the nearest 0.01 g. Stem height, root length, number of stolons, stolon lengths, number of flowers, and dry weights of modules were all recorded on a per pot (sample) basis.

Field study

The field study consisted of 30 one-meter square plots containing primarily (see discussion) *M. vimineum.*

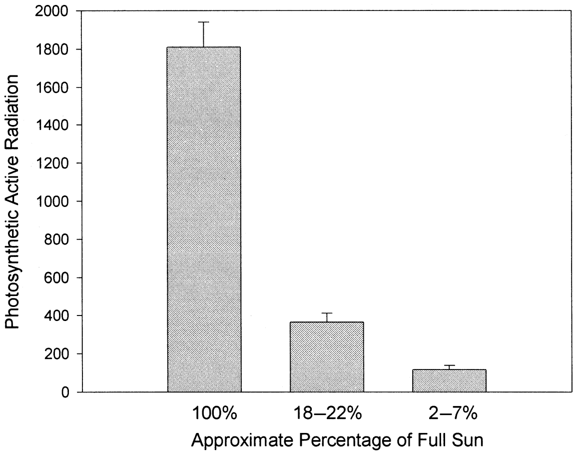

Figure 1. Mean photosynthetically active radiation from field plots for the three environmental habitats of *M. vimineum* (i.e., 100%, 18–22%, and 2–7% full sun). Data represent the mean and standard deviation of three visits to each of the plots and ten replicates for each shading level.

Plots were selected by locating ten full sun plots, ten approximately 18–22% full sun plots, and ten approximately 2–7% full sun plots. At least three separate measurements of PAR using a LI-191SA Line Quantum Sensor at different periods during the day were used to determine the percentage of light each plot received (Figure 1). The plots were established at Meeman Biological Station (35°50′ N, 89°50′ W), Ames Plantation (34°90′ N, 88°40′ W), and Shelby Farms (35°10′ N, 89°50′ W). All herbaceous and woody taxa were recorded at the beginning of the experiment in May 1999 and at the harvest of the field plots in September 1999. Three cores 7.62 cm in diameter and 30.48 cm deep were harvested in each plot when *M. vimineum* began to flower. The plants were separated into modules and dried at 60 °C for 48 h and weighed to the nearest 0.01 g.

Data analysis

Data used were the proportion of biomass allocated to the various plant modules as a measure of resource allocation. Percentage data were arcsine transformed prior to analysis (Zar 1984). Multivariate analysis of

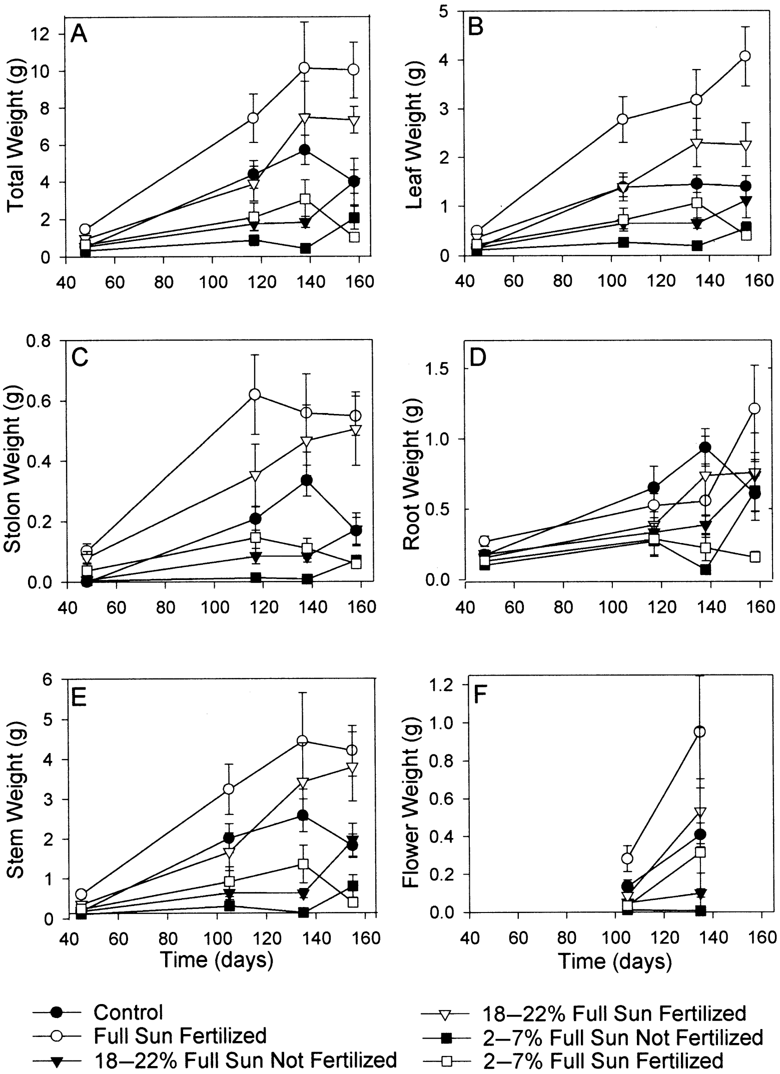

Figure 2. Total dry weight (represented by the mean and standard error) and dry weights of *M. vimineum* plant modules (i.e., leaf, stem, stolon, root, and flower) from harvest one through harvest four (day 48, 117, 138, and 158) from the greenhouse. Treatments consisted of three levels of shading and two levels of nutrients. Data are g O.D.W.

variance (MANOVA) was used to test the hypothesis that resource allocation was not affected by nutrients or shading. If the Pillai's Trace statistic in the MANOVA ($\alpha = 0.05$) conveyed a significant result, treatment effects were examined using analyses of variance (ANOVA). The protected ANOVAs ($\alpha = 0.05$) used four orthogonal contrasts to examine how differences in environmental conditions affected the plasticity of *M. vimineum* resource allocation. MANOVA and ANOVA were carried out using the Statistical Analysis System (SAS 2000) package.

Results

Greenhouse results

As expected, total plant biomass of *M. vimineum* increased from the first harvest to the fourth with fertilization (Pillai's Trace: $F = 11.19$, $P = 0.0001$) and decreased with shading (Pillai's Trace: $F = 2.48$, $P = 0.007$). Dry weights of the plant modules (Figure 2) generally increased throughout the experiment with only slight inhibition due to shading. There was a significant interaction between fertilizing and shading (Pillai's Trace: $F = 3.86$, $P = 0.0001$).

Leaf weight, stem weight, and total weight were significantly less under heavy shading (2–7% full sun) compared to full sun (Table 1, Figure 2). Shading also significantly decreased the number of stolons produced (Figure 3C). Fertilization had the opposite effect, resulting in higher weights and numbers of stolons produced. There was a notable difference of stem height ($P = 0.027$) in full sun *versus* shaded plants (Figure 3B).

The third harvest was analyzed alone due to the presence of all plant modules, including flowers (Figure 4). The percent allocation of resources to the various plant parts, including reproductive bodies, differed significantly due to fertilization (Pillai's Trace: $F = 12.36$, $P = 0.0001$), shading (Pillai's Trace: $F = 5.11$, $P = 0.0001$), and their interaction (Pillai's Trace: $F = 4.08$, $P = 0.0001$). The majority of resources were allocated to stems and leaves regardless of treatment (Figure 4). The proportion of carbon allocated to roots was greater in the control than the heavily shaded fertilized plants (Table 2, Figure 4). Conversely, the proportion of carbon invested in leaves in control plants was significantly less than in the heavily shaded fertilized plants ($P = 0.0012$). When compared to shaded plants, the control plants had greater root : shoot ratios ($P = 0.0027$), greater flower production ($P = 0.0396$), and greater stolon numbers ($P = 0.015$), but less leaf ($P = 0.0001$) and stem ($P = 0.018$) biomass (Figure 4).

The highest overall flower and stolon biomass occurred in the full sun fertilized treatment (Figure 4B) while the highest percent flower weight to total plant weight was in the control group (Figure 4A). The largest percent stolon yield to total plant yield was in the 18–22% full sun fertilized group (Figure 4D). Overall, both asexual and sexual reproduction was reduced in stressed environments. However, reproductive success was maintained in shaded habitats with the addition of nutrients (Figure 4A vs. 4F).

Table 1. Analysis of variance (ANOVA) orthogonal contrast statement F-statistic and P-values for greenhouse experiment of *M. vimineum* under three levels of shading (100%, 18–22%, and 2–7% full sun) and two levels of nutrients (fertilized or not fertilized). Analysis based on weights (g O.D.W.).

Variable	F	$P > F$
Total weight	6.83	0.0001
Control *versus* fertilized	13.61	0.0005
Control *versus* shaded	15.08	0.0003
No shade *versus* 2–7% shade	7.09	0.0102
Leaf weight	8.98	0.0001
Control *versus* fertilized	22.16	0.0001
Control *versus* shaded	15.74	0.0002
No shade *versus* 2–7% shade	16.62	0.0192
Stem weight	6.07	0.0002
Control *versus* fertilized	12.43	0.0009
Control *versus* shaded	12.96	0.0007
No shade *versus* 2–7% shade	6.39	0.0144
Root weight	5.12	0.0006
Control *versus* fertilized	1.84	0.1800
Control *versus* shaded	17.16	0.0001
No shade *versus* 2–7% shade	12.82	0.0007
Number of stolons	9.03	0.0001
Control *versus* fertilized	16.48	0.0002
Control *versus* shaded	21.07	0.0001
No shade *versus* 2–7% shade	8.65	0.0049
Stem height	6.52	0.0001
Control *versus* fertilized	7.36	0.0091
Control *versus* shaded	5.19	0.0270
No shade *versus* 2–7% shade	23.06	0.0001
Root to shoot ratios	3.77	0.0054
Control *versus* fertilized	12.97	0.0007
Control *versus* shaded	0.20	0.6592
No shade *versus* 2–7% shade	0.36	0.5513

Field results

Total plant biomass of the field plots followed a pattern similar to the greenhouse experiment (Figure 5A).

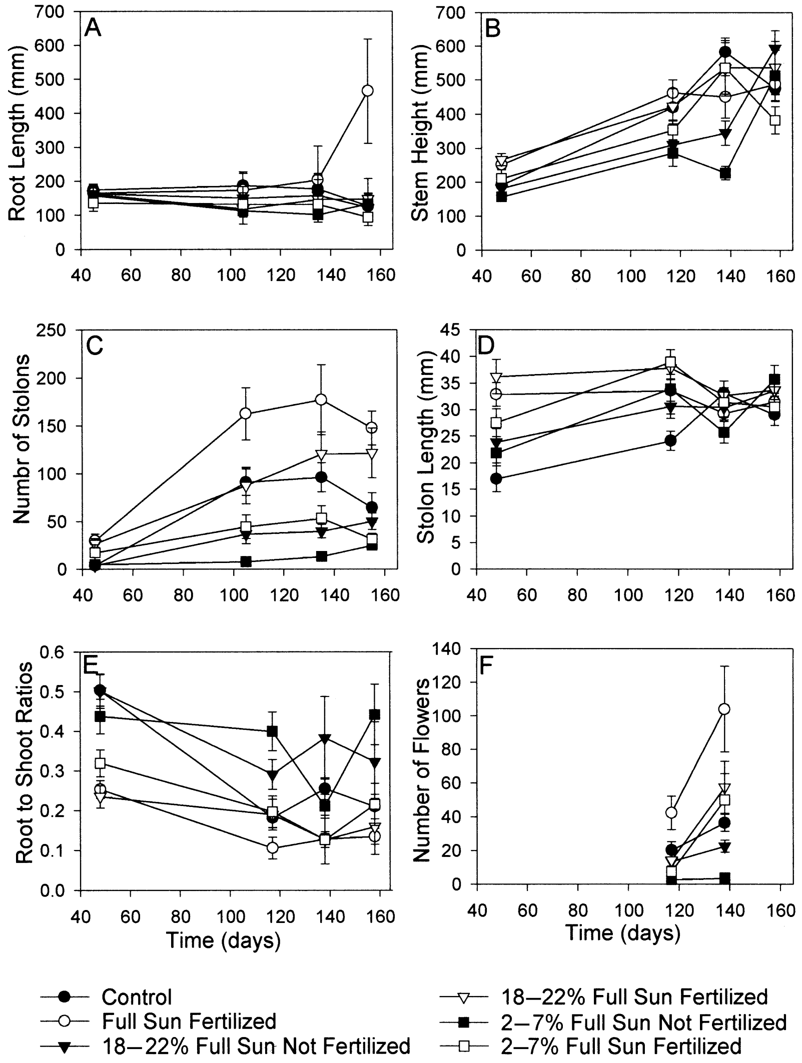

Figure 3. Root : shoot ratio and the lengths and numbers of various *M. vimineum* modules (i.e., root, stem, stolon, and flower) are shown from harvest one through harvest four (day 48, 117, 138, and 158) from the greenhouse. Data are means and standard errors. Treatments consisted of three levels of shading and two levels of nutrients.

However, no significant differences in resource allocation were found for any shading effect (Pillai's Trace: $F = 1.01$, $P = 0.4308$). Competition may be one factor explaining the lack of significance (see Discussion for associated plant taxa). The 100% full sun plots had an average species richness of 7.8, while the 18–22% and the 2–7% full sun plots had lower average species richness values of 3.6 and 4.4, respectively.

The plots that received 100% full sun produced the most total biomass, with the greatest biomass in the leaves and stems (Figure 5A). *M. vimineum* (Figure 5B) followed a general trend of a higher proportion of leaf biomass (to total biomass) and lower stem biomass (to total biomass) as shading increased. In addition, stolon production increased as light decreased.

Discussion

Microstegium vimineum has many characteristics typical of invasive exotic species and disturbance adapted species: (1) plasticity to environmental conditions, (2) annual life history, (3) high seed production, (3) lack of predators or pathogens, and (4) clonal growth to forage for resources (Baruch and Gomez 1996; Rejmánek and Richardson 1996). We showed

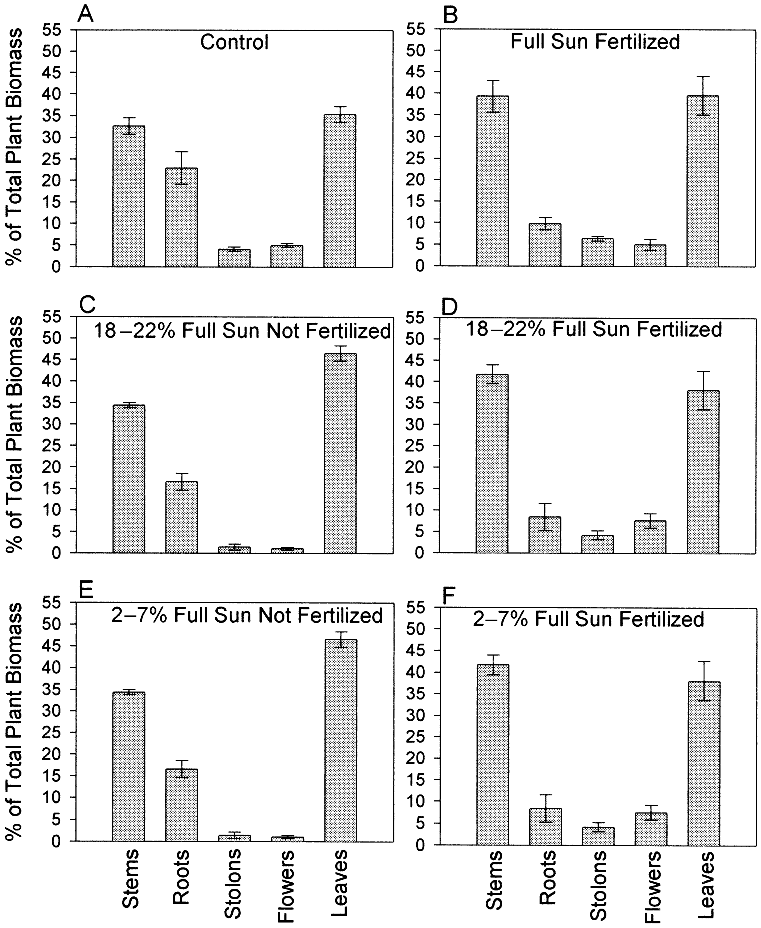

Figure 4. Mean (with standard errors) proportion of biomass allocated to the various plant modules from the third harvest (day 138) of *M. vimineum* in the greenhouse. The proportion was calculated as a percent of the total plant biomass produced under each of the six shading and fertilizer treatment conditions.

that *M. vimineum* has the plasticity to allocate resources differently in response to environmental variation, as do other species (Slade and Hutchings 1987; Cain 1994). Generally, the plants receiving the most light and nutrients were able to photosynthesize and produce the most biomass and reproductive effort. However, when plants were stressed (mainly due to nutrient deficiency), the shift of biomass allocation clearly demonstrated the plasticity of this species, which has been shown to respond both physiologically (Horton and Neufeld 1998) and morphologically (this study; Williams 1998). Indeed, it is expected that suites of characters will change rather than a species expressing a single character response to environmental alterations (Chapin et al. 1993). In *M. vimineum*, certain plastic responses suggest greater competitiveness and invasion potential.

Specifically, allocation expended to shoot production (i.e., leaves and stems) increased in shaded habitats to maximize photosynthetic capability. Since no height difference occurred across the treatments, we assume that the increased shoot biomass was in either leaf surface area or stem diameter. To maximize competitive ability where light is limited, some plants alter growth by: (1) allocating more resources to stems to avoid shading, (2) allocating more resources to leaves to receive more light (Abrahamson and Caswell 1982), (3) increasing chlorophyll per unit leaf weight, or (4) operating under a reduced respiration rate (Chapin et al. 1993; Crawley 1997).

We predicted that reproduction would vary based on environment (Meekins and McCarthy 2001). Sexual and asexual reproduction was greatest in full sun. Shading decreased and fertilization increased biomass

Table 2. Analysis of variance (ANOVA) arcsine transformation F-statistic and P-values for greenhouse experiment of *M. vimineum* under three levels of shading (100%, 18–22%, and 2–7% full sun) and two levels of nutrients (fertilized or not fertilized). Analysis based on proportion of total weight (g O.D.W.).

Variable	F	$P > F$
Leaf weight	7.41	0.0001
Control *versus* fertilized	0.54	0.4655
Control *versus* shaded	19.39	0.0001
No shade *versus* 2–7% shade	34.87	0.0001
Control *versus* fertilized/2–7% shade	11.73	0.0012
Stem weight	4.55	0.0016
Control *versus* fertilized	5.24	0.0260
Control *versus* shaded	10.84	0.0018
No shade *versus* 2–7% shade	9.55	0.0032
Control *versus* fertilized/2–7% shade	0.45	0.5033
Root weight	6.86	0.0001
Control *versus* fertilized	29.72	0.0001
Control *versus* shaded	0.06	0.8030
No shade *versus* 2–7% shade	0.09	0.7634
Control *versus* fertilized/2–7% shade	14.07	0.0004
Stolon weight	11.37	0.0001
Control *versus* fertilized	11.21	0.0015
Control *versus* shaded	12.89	0.0007
No shade *versus* 2–7% shade	36.24	0.0001
Control *versus* fertilized/2–7% shade	3.36	0.0725
Flower weight	6.26	0.0001
Control *versus* fertilized	4.45	0.0396
Control *versus* shaded	9.54	0.0032
No shade *versus* 2–7% shade	22.55	0.0001
Control *versus* fertilized/2–7% shade	0.30	0.5870

of reproductive structures. Contrary to our hypothesis, percent allocation to stolons was greater than to flowers in fertilized, full sun conditions, while allocation to flowers was greatest in shaded and fertilized conditions; although overall differences were small. The opposite trend occurred in non-fertilized plants. However, stolons and flowers were produced in all treatments, demonstrating reproductive plasticity (Williams 1998). Meekins and McCarthy (2001) found similar reproductive plasticity in the invasive exotic *Alliaria petiolata* (Bieb.) Cavara & Grande. In addition, there was little difference in percent allocation due to shading when plots were fertilized. The data suggest *M. vimineum* is capable of invading a wide variety of environments, but the environment will play a role in invasion success (Hobbs and Humpheries 1994; Burke and Grime 1996).

Resource allocation patterns of the greenhouse experiment resemble the field study except for a gradual shift in shoot biomass in the field from stems to leaves as light decreased. Our observations suggest field plants receiving 100% full sun were competing with several other grass and herbaceous species while shaded *M. vimineum* plants experienced generally lower competition (Horton and Neufeld 1998). Williams (1998) found a negative correlation between the biomass of *M. vimineum* individuals and the biomass of adjacent interspecific individuals. Species largely associated with *M. vimineum* in our full sun plots included *Polygonum* spp. and *Ambrosia* spp. The predominant associations under 2–7% full sun plots were *Parthenocissus quinquefolia* Planchon, *Laportea canadensis* (L.) Swartz and *Toxicodendron radicans* (L.) Kuntze, generally of much less density. *M. vimineum* put more resources in stem height growth than in leaves in field plots to reach greater heights as they competed for light. The plants under the canopy, on the other hand, produced more leaves to capture light. We did not study competition, but these results suggest the need for research examining exotic species plasticity relative to competition.

Explicit knowledge of the effects and interactions of factors that influence reproductive potential is required for predicting spread rates (Higgens et al. 1996). We predicted that the C_4 grass (typically light demanding), *M. vimineum*, compensates for low light levels by utilizing available soil nutrients in its typical floodplain habitat. Plants physiologically and morphologically compensate for drought stress (Tjoelker and Luxmoore 1991; Green and Mitchell 1992) and loss of tissue from herbivory (Wallace and Mako 1993) when ample nutrients are present. When low light floodplain shaded habitats were mimicked in the greenhouse, *M. vimineum* utilized soil nutrients to compensate for limited light. This observation was consistent with field data that showed that asexual plant spread was proportionally higher on a total plant basis in low light habitats. The sexual reproduction of this exotic invader seems to be successful as long as either a light or a nutrient source is present. However, research is needed to examine the long-term population fitness of *M. vimineum* rather than assuming fitness from reproductive structures.

The life history of invasive species that are successful in new habitats is an important characteristic to use in order to be able to predict the ability of a species to invade elsewhere (Reichard and Hamilton 1997; Parker et al. 1999). Our research shows that *M. vimineum* is an excellent example of the plastic abilities of invasive species, switching its allocation of resources in an effort to maximize growth and reproduction. In addition, the

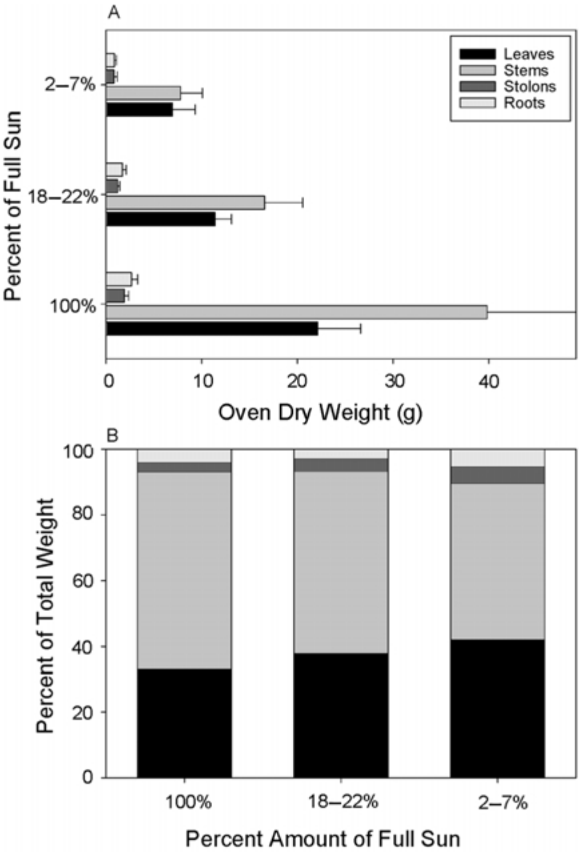

Figure 5. Mean (and standard error) amount of biomass allocated to the leaves, stems, stolons and roots for the three light treatments from the field study of *M. vimineum* as (A) total biomass allocated (g O.D.W.) and as (B) a proportion of the total weight produced.

plasticity of *M. vimineum* is increased through compensation (shading was less stressful with adequate nutrients), and thus allows *M. vimineum* to spread under a variety of environmental conditions. Experimental work examining plasticity (morphological and physiological) in relation to competition and compensatory effects is needed to strengthen our understanding of invasion potential.

Acknowledgements

The authors would like to thank Philip Robertson, James Luken, and two anonymous reviewers for their helpful remarks rendering a greatly improved manuscript. We thank the Edward J. Meeman Biological Field Station, Shelby Farms, and Ames Plantation for allowing us to establish plots on their grounds.

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