Two invaders in the same forest: comparisons of photosynthesis, herbivory, and competitive ability

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Abstract. The conditions that allow invasion by one plant species may well do the same for other non-native species; consequently the primary interactions between an invasive plant and other plant species in the community are likely to be with other invasives. For example, the biennial herb *Alliaria petiolata* (garlic mustard) and the annual grass *Microstegium vimineum* (Japanese stilt-grass) are two non-native plant species that spread into forests in the eastern U.S.A. Both grow in a wide range of light environments and colonize together in mixed stands. Study plots with both species present were established at Washington Crossing State Park in New Jersey. Cover of *M. vimineum* was greater per plot than cover of *A. petiolata* and increased over the course of the study. In July and September, *M. vimineum* had greater mean photosynthesis rates than *A. petiolata*. However, *A. petiolata* matched those higher rates during its rapid spring growth, measured in April before *M. vimineum* had germinated. In a greenhouse experiment of competition with a native phytometer under different shade treatments, *M. vimineum* exhibited higher photosynthesis rates, as well as the ability to increase photosynthesis at a greater rate when exposed to increased light levels, suggesting that it may have an advantage over *A. petiolata* in the forest by more readily utilizing high light patches. However, *A. petiolata* had greater overall mass than *M. vimineum*, due to root growth, in both light and shaded treatments. Finally, herbivory damage in a field experiment was less severe for *M. vimineum*, and its photosynthesis rate, growth and survival were greater. The two species appear to utilize different strategies for invasion and it seems that *M. vimineum* is the superior invader. Comparing the ecology of co-occurring non-native species within an ecosystem can be helpful for creating management strategies in areas where simultaneous invasions threaten native biodiversity.

The two invaders growing together; *M. vimineum* on left, *A. petiolata* on right.

INTRODUCTION

Ecological conditions that allow invasion by one non-native species often promote the simultaneous spread of other non-natives, resulting in communities that increasingly harbor multiple invasive plant species that may be co-dominant. Comparison of such co-occurring species has become a necessary tool as we seek to understand the ecology of modern plant communities in the fragmented landscape. Herb layer communities in mid-Atlantic region forests are a case in point, particularly in severely affected forests where the only species of notable abundance may be a handful of invasive non-natives. Two species often found together in these forests are *Alliaria petiolata* (garlic mustard) and *Microstegium vimineum* (Japanese stilt grass) and they are often the most abundant components of the herb layer. We made explicit comparisons of several key aspects of the ecology of these two species in order to predict their future spread, including association with light, photosynthesis rates, susceptibility to natural enemies, and competitive ability. Such comparisons could be very valuable for prioritizing management decisions in the common scenario where more than one invasive plant species presents simultaneous problems.

METHODS

Natural community study in 2001, 2002, and 2005. 28 one-m^2 plots were set up in Washington Crossing State Park (WCR), Titusville, NJ: 4 each on 7 transects. Plots were selected from all plots on the transect where *A. petiolata* and *M. vimineum* grew together, choosing the two with highest and the two with lowest PAR (photosynthetically active radiation) in order to include widest possible light range. **Variables**: percent cover of both species in 2001 and 2005, % full-sun PAR, photosynthesis rate with Li-Cor 6400 (a portable IRGA) in 2002.

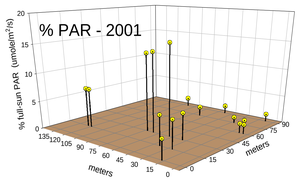
Greenhouse experiment, 2002. 280 pots were arranged in 7 blocks of 40 each, with each pot planted with field collected seed: half had one phytometer (*Eupatorium rugosum*, a co-occurring native herb) plus one *A. petiolata* ; the other half had the phytometer plus one *M. vimineum*. Half of each group were placed under individual pot-sized shade cloths. Data were collected after 2 months. **Variables**: phytometer biomass, invasive shoot and root biomass and photosynthesis rate at 84 and 1000 PAR (equivalent to the shaded and unshaded treatments).

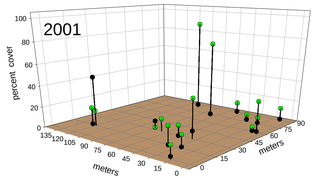
Field experiment, 2004. Seedlings of both invasives were grown in the greenhouse from field-collected seed, transplanted into three forests in central New Jersey, with 40 of each species in each forest, and followed for one growing season. **Variables**: photosynthesis rate, leaf herbivory, survival, final root and shoot biomass.

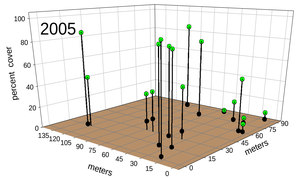
RESULTS

. . . . Natural community . . . .

Right and below: 2001 percent cover of *A. petiolata* in sampled plots averaged 9.9 % and *M. vimineum* averaged 36.2%. Light levels were variable across the sampled plots in 2001, but neither species' distribution was related to light level. The 2005 census showed that *M. vimineum* cover had increased greatly while *A. petiolata* had decreased. Percent cover of *A. petiolata* in 2005 averaged 5% and *M. vimineum* averaged 52%. (Figures show only plots that were relocated in 2005).

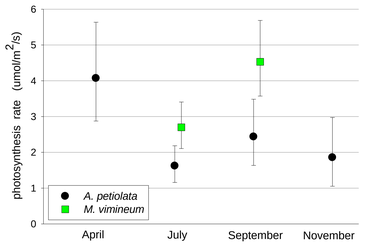






• *Alliaria petiolata* • *Microstegium vimineum*

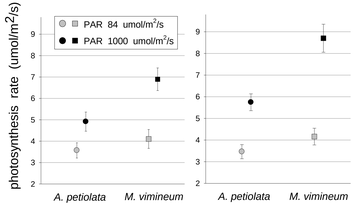
Right: Average photosynthesis rate for *M. vimineum* exceeded that of *A. petiolata* in July (ANOVA: F=24.45; df=1,49; P<0.0001), even though the PAR values recorded at the position of the plants did not differ between species. Similar results were seen in September (F=7.37; df=1,32; P=0.01). However, in the early spring, when *A. petiolata* was growing very quickly and before *M. vimineum* had germinated, *A. petiolata* exhibited photosynthesis rates as high as that of *M. vimineum* during summer.



(Means ± 95% CL; n from left to right: 23, 27, 36, 16, 24, 16)

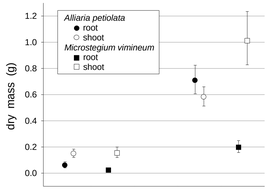
. . . . . .Greenhouse experiment . . . . . .

Right: *M. vimineum* photosynthesized at a higher rate than *A. petiolata* at PAR 1000, but at PAR 84 there was no difference between the species' rates (ANOVA: SPECIES X PAR F=2.90; df=1,235; P=0.09). The percent rate increase when PAR increased from 84 to 1000 was significantly greater in *M. vimineum* (ANOVA: SPECIES F=9.68; df=1,111; P=0.002), and for both species the increase was greater in unshaded plants (SHADING F=5.43; df=1,111; P=0.022)



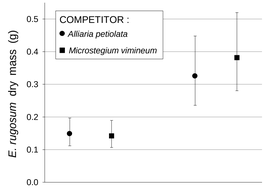
(Means ± 95% CL; n from left to right: 29, 29, 35, 35, 32, 32, 31, 31)

Right: Total dry mass (root + shoot) did not differ between *A. petiolata* and *M. vimineum* and shading decreased final total mass in both species (ANOVA: SPECIES F=0.65; df=1,183; ns. SHADING F=354.29; df=1,183; P<0.0001). Under shade cloth both species had similar negative root:shoot ratios, but with higher available light resources (no shade cloth) *A. petiolata* allocated somewhat more to roots while *M. vimineum* allocated much more to shoots (ANOVA: SPECIES X SHADING F=26.75; df=1,183; P<0.0001).



(Back-transformed means ± 95% CL; n from left to right: 46, 46, 59, 59, 53, 53, 54, 54)

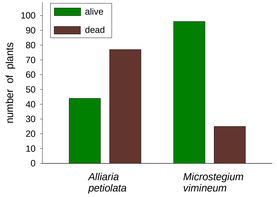
Right: *A. petiolata* and *M. vimineum* showed no difference in competitive effects on the phytometer they grew with in the pots, *Eupatorium rugosum*. The phytometer had greater final total dry mass when grown without shade cloth, but the identity of the species with which it competed made no difference in its final size (ANOVA: SHADING F=34.26; df=1,183; P<0.0001. SPECIES F=0.37, df=1,183; ns).



(Back-transformed means ± 95% CL; n from left to right: 46, 59, 53, 54)

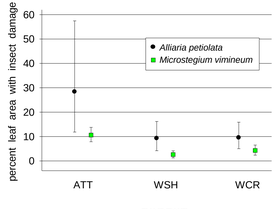
. . . . . Field experiment

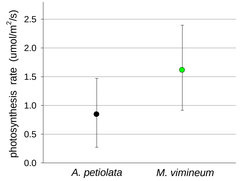
Right: Mortality of experimentally planted *A. petiolata* plants was greater than that of *M. vimineum*. About two-thirds of the *A. petiolata* plants died, but only about a quarter of the *M. vimineum* plants died (G-test for heterogeneity, G=47.58; df=1; P<0.0001).



Right: Leaf damage classified as insect herbivory was higher on *A. petiolata* than on *M. vimineum* (ANOVA: SPECIES F=27.95; df=1,134; P<0.0001)

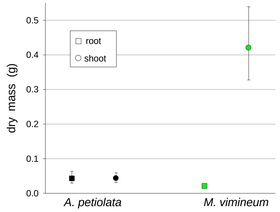
(Back-transformed means ± 95% CL; n from left to right: 11, 19, 15, 27, 18, 35)





Above: Photosynthesis rates were greater on average for *M. vimineum* than for *A. petiolata* (ANOVA: SPECIES F=3.52; df=1,83; P=0.064).

(Back-transformed means ± 95% CL; n from left to right: 41, 48)



Above: *M. vimineum* accumulated greater total mass than *A. petiolata* and had much lower root:shoot ratio (ANOVA: SPECIES F=334.45, df=1,138, P<0.0001).

(Back-transformed means ± 95% CL; n from left to right: 39,39,106,106)

DISCUSSION

The two non-native invasive herbs *Alliaria petiolata* and *Microstegium vimineum* often grow side-by-side in the same forests, where they both threaten native species. Our greenhouse experiment indicated that they had similar competitive effects on a native test species and both grew in a wide range of light levels, but our other comparisons suggest that *M. vimineum* is ecologically superior compared to *A. petiolata*. In our natural community study *M. vimineum* was more abundant and increased over four years, while *A. petiolata* declined. The two species utilize different life history strategies; *A. petiolata* is a biennial and must allocate much of its first-year growth to roots while *M. vimineum* is an annual that grows rapidly throughout the summer and allocates mostly to shoots, easily overtopping first-year *A. petiolata* rosettes. *M. vimineum* consistently generated greater photosynthesis rates, with the exception of early spring when *A. petiolata* rates equaled those of *M. vimineum* in the summer. The greenhouse experiment showed that *M. vimineum* was better at utilizing a rapid increase in light level such as occurs in a sunfleck. This should help *M. vimineum* grow well under closed canopy, along with its C_4 photosynthesis pathway allowing efficient photosynthesis even in the hottest, driest summer weather. *M. vimineum* also experienced much less herbivory than *A. petiolata*. Along with superior summer photosynthesis, this may explain why its mortality also was much lower. Overall, our results indicate that *M. vimineum* has the greater potential for ecological success and resulting negative effects on the native community.

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