Biol Invasions (2010) 12:721–724
DOI 10.1007/s10530-009-9480-x

INVASION NOTE

Native, insect herbivore communities derive a significant proportion of their carbon from a widespread invader of forest understories

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Received: 3 February 2009 / Accepted: 6 May 2009 / Published online: 21 May 2009

Abstract Research on natural enemies demonstrates the potential for exotic plants to be integrated into foodwebs through the activities of native herbivores. The quantitative importance of exotics as a food resource to herbivores is more difficult to ascertain. In addition, some widespread invaders appear to have minimal herbivore loads. *Microstegium vimineum* is one example. It is an annual, C_4 grass that invades forest understories and is widespread across the eastern US. Its invasion alters the structure and composition of forests. We sampled invertebrates in a tree-canopy gap and under canopy area, and used the unique carbon isotope value of *M. vimineum* to estimate the quantitative importance of the invader as a food resource relative to native plants. Seven of the eight invertebrate species derived on average >35% of their biomass carbon from *M. vimineum*, and some individuals representing both 'chewing' and 'sucking' feeding guilds derived their biomass carbon exclusively from *M. vimineum*. Our results show that *M. vimineum* can be a significant food resource for a multi-species, multi-guild, assemblage of native, invertebrate herbivores. Future work is required to assess whether *M. vimineum* is acquiring herbivores in other parts of its introduced range, and if so what might be the ecological consequences.

Keywords Enemy release hypothesis · Exotic species · Grass invasion · Grasshoppers · Hardwood forests · Herbivory · Invertebrate herbivores · Japanese stilt grass · *Microstegium vimineum* · Nepalese browntop

Introduction

Exotic plant species can be integrated into native foodwebs through feeding activities of native herbivores. The quantitative importance of exotic plant species as a food resource to herbivores is, however, difficult to ascertain. In addition, some widespread, invasive plant species appear to have minimal herbivore loads. *Microstegium vimineum* (Trin.) Camus is one example. There is no evidence that it is browsed by deer (Webster et al. 2008) or other

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vertebrates, and invertebrate herbivore damage rates on *M. vimineum* are low, ranging from 0.4 to <10% of leaf tissue removed (Morrison et al. 2007; Sanders et al. 2004). It invades forest understories across 25 US states (http:/plants.usda.gov/) and, given the extent of its distribution, understanding its impacts is important (Morrison et al. 2007). These include alterations to ecosystem structure (Baiser et al. 2008), plant and faunal communities (Baiser et al. 2008; Civitello et al. 2008; Oswalt et al. 2007; Vidra et al. 2006), soil properties (Kourtev et al. 2002), and success of other invasive plants (Belote and Weltzin 2006; Morrison et al. 2007). Whether its apparent lack of herbivores explains its expanding distribution and consequent impacts is unknown, as is its relevance to green foodwebs within its introduced range. Here, we report on an opportunistic study, based on the observation that two, visually abundant, species of Orthoptera resided on *M. vimineum* foliage in an invaded canopy gap. Given that *M. vimineum* is the only plant to utilize the C_4-photosynthetic pathway at the site, we reasoned that if the Orthoptera were feeding on *M. vimineum* then they would have a stable carbon (C) isotope value distinct from that of the foodweb based on native plants, which all use the C_3-photosynthetic pathway (see Fry 2006).

Materials and methods

A tree-canopy gap and an under canopy habitat were identified within a rapidly progressing *M. vimineum* invasion in a riparian forest within the Whitehall Experimental Forest (WEF), Athens, GA, USA (N 33°53.27′ W 83°21.93′). Anecdotal reports indicate *M. vimineum* established within the WEF ~15 years ago. The forest overstory is composed of *Acer rubrum*, *Quercus nigra*, *Platanus occidentalis*, and *Liquidambar styraciflua*. The uninvaded areas of the site are generally depauperate in understory plants (<5% cover) but *M. vimineum* forms a continuous lawn.

We spent 2 person hours per habitat, on September 15th 2008, using a sweep-net and hands to catch invertebrates located in the understories. Next, for *M. vimineum* we took five leaves from 10 individuals in each habitat and for native plants we collected five leaves from any native trees and herbs in the understory that exhibited signs of invertebrate leaf-chewers. Plant and invertebrate materials were dried at 65°C to constant mass, ball-milled to a fine powder and then weighed into tin cups for isotope determinations.

Microstegium vimineum has a C_4-photosynthetic value and the difference in the C isotope composition from the natives, which use the C_3-pathway, is sufficient to discriminate sources (see Fry 2006). The proportion of C derived from *M. vimineum* was calculated as: $C_{M.\ vimineum\ \mathrm{derived}} = (\delta^{13}C_{\mathrm{invert}} - \delta^{13}C_{\mathrm{native}})/(\delta^{13}C_{M.\ vimineum} - \delta^{13}C_{\mathrm{native}})$, where $\delta^{13}C_{\mathrm{invert}}$ is the $\delta^{13}C$ value of the biomass for each invertebrate, $\delta^{13}C_{\mathrm{native}}$ is the mean $\delta^{13}C$ value of the native leaf tissues and $\delta^{13}C_{M.\ vimineum}$ is the mean value for the *M. vimineum* tissues. The $\delta^{13}C$ values were determined using continuous-flow isotope-ratio mass spectrometry (Thermo, San Jose, CA, USA).

Results and discussion

In both the canopy gap and under canopy habitats we observed evidence of invertebrate herbivory on the leaf blades of *M. vimineum* (Fig. 1). There was a distinct difference in the behaviors and phenotypes of the invertebrates collected in each habitat. Those invertebrates in the canopy gap were highly active, attempting to avoid capture by large jumps (>1 m), and their dominant coloration was green. In contrast, those invertebrates in the under canopy habitat were cryptic and remained still when detected. They were

Fig. 1 A long-horned grasshopper (*Orchelimum* sp.) on the foliage of *M. vimineum*. Note the evidence of invertebrate leaf-chewing on the leaf-blade immediately to the right of the orthopteran

Table 1 Identification and percentage biomass carbon derived from *M. vimineum* of invertebrate herbivores found on *M. vimineum* foliage in Whitehall Experimental Forest, Georgia, USA. Habitats are a canopy gap (CG) or under canopy (UC) patch

Habitat patch	Invert. family, order, genus species	Life stage	Common family name	# Indv. sampled	δ^{13}C value of indv. (‰)	C derived from *M. vimineum* (%)
CG	Orthoptera, Acrididae, *Metaleptea brevicornis* (L.)	Adult	Short-horned grasshoppers	6	−19.24	71.7[e]
CG	Orthoptera, Tettigoniidae, *Orchelimum* sp.	Nymph	Katydids[c]	10	−24.32	46.7[e]
UC	Orthoptera, Tettigoniidae, *Neoconocephalus* sp.	Nymph	Katydids[c]	1	−14.89	99.1
UC	Orthoptera, Tettigoniidae, *Orchelimum* sp.	Adult	Katydids[c]	2[d]	−26.20	35.9
UC	Orthoptera, Gryllidae, *Gryllus* sp.	Immature	Crickets	1	−25.03	42.4
UC	Hemiptera, Coreidae, *Leptoglossus oppositus* (Say).	Adult	Leaf-footed bugs	1	−31.99	3.50
UC	Hemiptera, Largidae; *Largus* sp.[a]	Adult	Bordered plant bugs	1	−14.58	101[f]
UC	Hemiptera, Pentatomidae, *Dendrocoris* sp.[b]	Nymph	Stink bugs	1	−14.27	103[f]

Note that mean δ^{13}C values for native plants vs. *M. vimineum* were: −33.82 vs. −13.49 in the canopy gap; and −32.61 vs. −14.72 in the under canopy patch

[a] Probably *L. succinctus* (L.)

[b] *D. fruticola* (Berg.) or *D. humeralis* (Uhler)

[c] An alternative common family name for Katydids is 'Long-horned grasshoppers'

[d] Analyzed as a single, pooled sample

[e] Values across individuals ranged from 31.6 to 110%, and 33.4 to 104%, C derived from *M. vimineum* for *Metaleptea brevicornis* and the canopy gap *Orchelimum* sp., respectively

[f] Values >100% probably represent the influence of C isotope fractionation and/or variation in C isotope values of native plant and *M. vimineum* individuals

largely brown in coloration and located on the underside of *M. vimineum* leaves or on their stalks. Given these differences in behavior and coloration, the invertebrate herbivores in each habitat appeared to belong to distinct communities particular to their environments. Indeed, there was little overlap in the species sampled from each habitat (Table 1). Notably, more than twice as many invertebrate individuals were recovered in the open canopy habitat but these comprised only two species of Orthoptera (Table 1). In the under canopy habitat there were six species from orthopteran and hemipteran orders (Table 1), and these represented both 'leaf-chewers' (orthopteran species) and 'suckers' (hemipteran species). So, based on our sampling effort, the invertebrate herbivore community in the under canopy habitat was both more species diverse and of greater functional diversity (Table 1). All invertebrates recorded are either native or naturalized within the study site's locality.

All invertebrate species recovered (except *Leptoglossus oppositus*) derived a substantial fraction of their biomass C from *M. vimineum* (Table 1). There was pronounced variation in the amount of biomass C derived from *M. vimineum* between species and, in the canopy gap habitat where >1 individual of the same species was sampled, within a species (Table 1). Notably, some species and/or individuals appeared to derive their biomass C exclusively from *M. vimineum* and this was true for multiple feeding guilds, taxonomic orders, and life stages (Table 1).

We have been working within the *M. vimineum* invasion described here since the 2005 growing season. The accumulation of an indigenous, invertebrate, herbivore community by an exotic, plant invader appears a recent occurrence (i.e., in 2008) at our site. Although our inferences are limited to a single invasion of *M. vimineum* within a hardwood forest, we cautiously venture outside the boundaries of our study site to discuss the potential ecological significance of our findings. First, *M. vimineum* has invaded forests over a large portion of the eastern and southern US and has wide-ranging impacts (e.g., Baiser et al. 2008). Its distribution and impact on forest ecosystems alone necessitate it receive the attention by the ecological community which is being afforded to other plant invaders (see Morrison et al. 2007). An important research focus will be to ask how the acquisition of herbivores might alter these impacts on forest ecosystems. If the herbivory we observed is sustained in future growing seasons, one might hypothesize that acquisition of enemies might reduce *M. vimineum*'s abundance and potentially distribution. However, non-invaded areas of our forested site have a highly depauperate understory and so *M. vimineum* might actually increase herbivore pressure on native plants by providing a resource for the native herbivores to increase their population sizes. This might then increase the apparent competitive advantage of *M. vimineum*. Future work is required to assess the extent and magnitude of herbivory on *M. vimineum* across its introduced range and, if significant, what the ecological consequences might be for the invaded ecosystems.

Acknowledgments This research was supported by National Science Foundation funding to Coweeta LTER. Tom Maddox in the Odum School of Ecology performed isotope analyses.

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