Invader partitions ecological and evolutionary responses to above- and belowground herbivory

WEI HUANG,1,2 JULI CARRILLO,3 JIANQING DING,1,4 AND EVAN SIEMANN3

1Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074 China
2Graduate University of Chinese Academy of Sciences, Beijing 100049 China
3Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005 USA

Abstract. Interactions between above- and belowground herbivory may affect plant performance and structure communities. Though many studies have documented interactions of invasive plants and herbivores, none shows how above- and belowground herbivores interact to affect invasive plant performance. Here, in a common garden in China, we subjected genetically differentiated tallow trees (Triadica sebifera) from native (China) and invaded (United States) ranges to herbivory by aboveground adults and belowground larvae of a specialist beetle, Bikasha collaris. Overall, relative to plants from China, U.S. plants had greater total and aboveground mass, comparable belowground mass, lower resistance to both above- and belowground herbivory, and higher tolerance to aboveground herbivory only. Accordingly, aboveground adults had greater impacts on Chinese plants, but belowground larvae more strongly impacted U.S. plants. These results indicate that the invader may adopt an “aboveground first” strategy, allocating more resources aboveground in response to selection for increased competitive ability, which increases aboveground tolerance to herbivory. Furthermore, we found that adults facilitated larval success, and these feedbacks were stronger for U.S. plants, suggesting that aboveground feeding of adults may be associated with lower defenses and/or higher resources belowground in the invader. Therefore, plants may have evolved different responses to above- and belowground herbivory, which can affect invasion success and herbivore population dynamics. These findings may provide new insights for an effective biological control program against invasive plants.

Key words: aboveground herbivory; belowground herbivory; Bikasha collaris; China; flea beetle; herbivores; plant invasion; resistance; resource allocation; tallow tree; tolerance; Triadica sebifera.

INTRODUCTION

Plants are consumed by both above- and belowground herbivores. Recent studies reveal that complex yet poorly understood interactions between above- and belowground herbivory may affect individual fitness and structure communities (Heil 2011, van Dam and Heil 2011); however, little information is available in the contexts of evolutionary and ecological timescales (Bardgett and Wardle 2003, Wardle et al. 2004, Bezemer and van Dam 2005, Erb et al. 2008, van der Putten et al. 2009, Knochel et al. 2010). The effects of escape from aboveground specialist herbivores on invasive plant success and traits are relatively well studied (Liu and Stiling 2006, Mitchell et al. 2006). However, there has been less focus on belowground herbivores, with much of the research to date focused on development of biological control (Blossey and Hunt-Joshi 2003) and few studies of the importance of belowground specialist herbivory in plant invasion success ( Müller-Schärer et al. 2004, Ridenour et al. 2008, van der Putten et al. 2009). Furthermore, since plants may evolve to allocate their defenses in a way that maximizes their fitness (Stamp 2003), understanding above- and belowground interactions in invasive plants may help reveal the mechanisms by which the plants allocate resources for growth and defense between above- and belowground to improve their performance in the introduced range, as a response to novel insect communities. Though several theories have been developed to explain invasion success (e.g., release from natural enemy [ERH], evolution of increased competitive ability [EICA] hypothesis, novel weapons, see Mitchell et al. 2006), no studies have addressed these critical issues.

Native to China, tallow tree, Triadica sebifera (L.) Small (synonym: Sapium sebiferum; hereafter “tallow”; Euphorbiaceae) is now a widespread plant invader in the southeastern United States (Bruce et al. 1997). Previous studies suggest that tallow has evolved to be a fast-growing and less herbivore-resistant plant in response to low herbivore loads in its introduced range (Siemann and Rogers 2001, 2003, Siemann et al. 2006),
providing evidence to support the EICA hypothesis (Blossey and Nötzold 1995). Recent studies also indicate that invasive populations of tallow have greater allocation aboveground and tolerate herbivory more effectively relative to native populations (Rogers and Siemann 2004, 2005, Zou et al. 2008a, b, Huang et al. 2010, Wang et al. 2011). However, no tests of EICA to date have examined interacting above- and belowground herbivores for any plant species (Bossdorf et al. 2005, Mitchell et al. 2006, Ridenour et al. 2008, van Dam 2009, van der Putten et al. 2009, Rapo et al. 2010).

Tallow suffers herbivory by more than 100 insect species in China (Zheng et al. 2005). In the introduced range, several generalists are found attacking tallow; all of them feed aboveground and no belowground herbivores have been reported. In China, the specialist flea beetle Bikasha collaris Baly (Coleoptera: Chrysomelidae) commonly reaches high densities and feeds both above- and belowground. The adults feed on mesophyll tissue of leaves, producing irregular pits, and larvae burrow into roots and feed internally, producing elongate tunnels. Bikasha collaris is multivoltine: the adult and larval life stages of different generations typically feed on the same plant at the same time (Zheng et al. 2005). Therefore, this is an intriguing model system to examine plant responses to the interactions among above- and belowground herbivores at ecological and evolutionary timescales (van Kleunen et al. 2010). For systems with differing above- and belowground herbivore species, their interactions may be affected by the sequence of herbivory, herbivore types, and their prior host plant species used (Erb et al. 2011, van Dam and Heil 2011).

Here we investigate the interactive effects of the aboveground adults and belowground larvae of *B. collaris* on tallow growth and the interactive effects of above- and belowground plant growth and defense on herbivore individual performance. We included both invasive and native tallow populations in our study to examine genetic differences in above- and belowground herbivore interactions. All previous studies on tallow only examined aboveground herbivores (e.g., Siemann and Rogers 2001, 2003b, c, Rogers and Siemann 2004, 2005, Zou et al. 2008a, b, Huang et al. 2010, Wang et al. 2011). Here we hypothesized that, compared to plants from native populations, plants from invasive populations would have lower resistance to both above- and belowground herbivores (herbivore release) and would be less impacted by aboveground herbivory than belowground herbivory (greater aboveground allocation).

**Material and Methods**

**Study system**

Tallow (*Triadica sebifera*) is a rapidly-growing, polycarpic tree. It is native to China and Japan and was first introduced to Georgia in the United States in the late 18th century for agricultural and ornamental purposes, then to Texas, Florida, and Louisiana in the early 20th century (Bruce et al. 1997). Currently, tallow seedlings and adult trees have become severe invaders that aggressively displace native plants and form monospecific stands in the southeastern United States (Bruce et al. 1997, Pattison and Mack 2008, Battaglia et al. 2009).

The flea beetle, *B. collaris* (see Plate 1), is a common insect herbivore attacking tallow in China (Zheng et al. 2005, Zou et al. 2008b). The adults feed on leaves, causing feeding scars, while the larvae feed on roots, forming elongate tunnels. Currently, this species is being investigated as a potential biological control agent for tallow. In the laboratory, adults oviposit in the soil 6.3 ± 0.3 d [mean ± SE] after mating and can lay eggs over multiple days. Eggs hatch in the dark and take 8.7 ± 0.1 d to incubate. Larvae take 17.9 ± 0.3 d to reach the pupal stage. Pupae take 8.6 ± 0.2 d to complete development. Preliminary host specificity tests indicate that *B. collaris* is a monophagous specialist that feeds exclusively on tallow, rejecting even congeners as a host plant (Huang et al. 2011).

**Seeds and seedlings**

We collected tallow seeds from six populations across southern China (hereafter, “native populations”) and six populations across the southeastern United States (hereafter, “invasive populations”) in late November 2008 (Appendix A). Recent molecular studies indicated that populations in the introduced range come from at least two distinct introduction events, with the original introduction to Georgia and South Carolina likely from a southern China population (the closest match in this study would be Guangdong). Later introductions to the United States are likely from the northeast part of tallow’s range (Jiangsu is the closest match in this study) (DeWalt et al. 2011). Therefore, we consider populations used in this experiment to be representatively native and invasive.

We collected seeds from 10–20 haphazardly selected tallow trees within each population. We removed the seed’s waxy coats by soaking the seeds in water with laundry detergent (10 g/L) for 2 d. To evaluate the potential impacts of seed provisioning on seedling performance, we weighed 20 seeds from each population. We detected no differences in the seed mass of native and invasive populations (*F*~1,10~ = 1.41, *P* = 0.26, nested ANOVA). We then buried the seeds in moist sand at a depth of 5–10 cm and placed them in a refrigerator (4°C).

We planted 100 seeds from each population for germination and initial growth on growing medium (50% topsoil and 50% sphagnum peat moss) in a greenhouse on 3 June 2009 (day 0). Such topsoil is generally slightly acidic (pH ~ 6.5). To eliminate potential adverse effects of build-up of host-specific soil biota, we collected topsoil from fields where no natural tallow trees grew. After four weeks of growth (day 28),
we selected similarly sized seedlings to transplant individually into pots (16 cm height, 25 cm diameter) containing growing medium. We then randomly arranged the seedlings in an outdoor common garden at the Wuhan Botanical Garden, Chinese Academy of Sciences, Hubei, China (30°32’ N, 114°24’ E). To eliminate potential negative effects of water limitation, pots were placed in 15 cm deep trenches and irrigated two or three times per week. In addition, to ensure that high temperatures did not negatively affect seedlings, the entire experiment was covered with a black polypropylene shade cloth 2 m above the ground. Finally, to exclude insect herbivory other than that from our experimental treatments, we enclosed each seedling in a nylon cage (100 cm height, 27 cm diameter) that was fitted tightly to the rim of each pot even when herbivores were not present as experimental treatments.

**Experimental design**

To examine relationships among above- and belowground resistance and tolerance and genetic variation in resistance and tolerance to each mode of feeding, a common garden experiment was conducted from July to October in 2009. The experiment was established as a 2 × 2 × 12 full factorial design incorporating two levels of aboveground herbivory (0 vs. 10 adults/seedling), two levels of belowground herbivory (0 vs. 10 larvae/seedling), and 12 tallow populations (six populations per range). There were three replicates for each combination and a total of 144 seedlings.

For aboveground herbivory, adults of *B. collaris* were obtained from the field near Wuhan Botanical Garden. The adults are usually found to consume 15–20% leaf area in natural conditions (J. Ding, personal observation; Zou et al. 2008a). Our previous study suggested that 10 beetles per plant may be the appropriate stocking level for such damage in 18 d and larvae are able to develop to pupal stage during this period (Huang et al. 2011). For belowground herbivory, larvae treatments were established as eggs due to the difficulty of manipulation of newly hatched larvae. To obtain eggs, naturally mating adults were transferred to 10-cm diameter petri dishes (one pair per petri dish) under laboratory conditions at 26–30°C, 50–70% relative humidity and with a 14-h photoperiod. Each petri dish contained corrugated moist filter paper as an artificial oviposition substrate and fresh leaves of tallow (Wuhan population) as food. The average number of first laid eggs per mating pair was 12. To ensure that sufficient newly laid eggs were collected simultaneously, collections were conducted on more than 120 pairs of mating adults.

One week after transplanting (day 35), we measured stem height, stem diameter, and number of leaves. No difference was detected in stem height ($F_{1,10} = 0.01, P = 0.92$), stem diameter ($F_{1,10} = 2.26, P = 0.16$), or number of leaves ($F_{1,10} = 0.51, P = 0.49$) between invasive and native populations. We randomly assigned seedlings to herbivory treatments. To establish belowground herbivory treatments, 10 newly laid eggs were transferred directly to a hole dug (3–4 cm deep, 1 cm diameter) in the soil at the base of each plant and covered with moist soil. Nine days later (day 44), which is approximately when eggs would hatch and larvae would begin feeding belowground, aboveground herbivory treatments were established by releasing 10 adults into cages. Adults were allowed to feed for 18 d and then removed (day 62). This procedure allowed above- and belowground herbivory to coincide as egg incubation time is 9 d and larval development time is 18 d. To prevent oviposition by adults in the soil and make above- and belowground herbivory experimentally independent, the nylon cage of each pot was sealed using string to the seedling stem.
below all leaves during the 18 days adults were present (in addition to being sealed around the pot rim). The control plants were also sealed with string. To assess aboveground herbivory and performance of aboveground herbivores, numbers of surviving adults were recorded and percentage of leaf area damaged was estimated for each seedling every two days. The percentage of leaf area damaged was determined by visual estimate (to the nearest 5%) for each leaf, then averaging the visual estimates for all damaged leaves. To assess belowground herbivory and performance of belowground herbivores, adults emerging from the soil were monitored and removed every two days. The number of emergent adults was recorded for each seedling. This procedure lasted 14 d (day 76), which was sufficient time for pupae to complete development. Subsequently, seedlings were allowed to regrow. Two months later (day 132), all aboveground plant material was clipped at the soil surface and roots were carefully washed. Above- and belowground plant parts were dried separately for 48 h at 80°C and weighed.

Statistical analyses
To examine the relationships among above- and belowground resistance and tolerance and genetic variation in resistance and tolerance to each mode of feeding, four-way mixed ANOVAs were performed on the plant growth results. The models included origin (native vs. invasive) and above- and belowground herbivory levels (0 vs. 10 insects per plant) as fixed effects and plant populations (six populations per range) nested within continent as the random effect. We used the variation among populations to test for significant effects of origin. In other words, the F tests for origin as a main effect used population nested in origin as the error term (resulting in $F_{1,10}$). The tests for interactive effects of origin and larval presence, origin and adult presence, or origin, larval presence, and adult presence used the corresponding term with population nested in origin as the error term. Tests for significant effects of larval presence, adult presence, and their interaction used the residual error term. We conducted adjusted means partial difference tests to examine differences among treatment levels for significant interaction terms. All data analyses were performed with the statistical analysis software SAS, version 9.1 (SAS Institute, Cary, North Carolina, USA).

Separate analyses were performed to determine variation in the belowground response variable number of larvae emerging as adults (three fixed effects, origin, adult presence, and their interaction; random effects, population nested in origin and its interaction with adult presence) and the aboveground response variables leaf area removed (square-root transformed) and number of adults surviving to the end of the aboveground herbivore treatment period (three fixed effects, origin, larval presence, and their interaction; random effects, population nested in origin and its interaction with larval presence). For these analyses of larval and adult responses, there were 72 data points each.

Tolerance to herbivory was assessed in a series of regressions. In these regressions, we fitted the origin and origin $\times$ damage terms but did not include intercept or damage terms so that a separate intercept and slope of mass vs. damage was fit for each origin. Then, contrasts were conducted to determine whether intercepts or slopes differed between origins.

Results
Overall, plants from the native range (China) had significantly lower total mass ($F_{1,10} = 10.48, P < 0.01$) and aboveground mass ($F_{1,10} = 14.09, P < 0.01$) than those from the invasive range (United States; Fig. 1; see Appendix B for full ANOVA table of plant response variables). For belowground mass, however, there was no significant difference between U.S. and Chinese plants ($F_{1,10} = 3.62, P = 0.09$; Fig. 1). This pattern was also reflected in a higher root:shoot ratio on average for Chinese plants compared to U.S. plants ($F_{1,10} = 10.42, P < 0.01$; Fig. 1).

Aboveground adults and belowground larvae each significantly reduced plant total mass (adults, $F_{1,96} = 182.87, P < 0.0001$; larvae, $F_{1,96} = 71.91, P < 0.0001$; Fig. 1). Adults more strongly reduced aboveground mass relative to belowground mass (significantly higher root:shoot ratio; $F_{1,96} = 24.34, P < 0.0001$; Fig. 1). In contrast, larvae more strongly reduced belowground mass (significantly lower root:shoot ratio; $F_{1,96} = 21.14, P < 0.0001$; Fig. 1). In addition, adult and larval herbivory had a significant interactive effect on plant mass ($F_{1,96} = 19.26, P < 0.0001$; partial difference tests, control $>$ larvae $>$ adult $>$ both). When both adults and larvae were present, plants had lower mass than predicted by the independent effects of each herbivore (Fig. 1).

Plant origin and adults had significant interactive effects on aboveground mass ($F_{1,10} = 7.09, P < 0.05$) and total mass ($F_{1,10} = 5.47, P < 0.05$). Adults more strongly impacted Chinese plants than U.S. plants (Fig. 1). Both aboveground mass and total mass were not significantly different for U.S. and Chinese plants without adults, but U.S. plants were significantly larger than Chinese plants when adults were present (partial difference test, $P < 0.05$; Fig. 1). Plant origin and larvae also had significant interactive effects on aboveground mass ($F_{1,10} = 7.89, P < 0.05$) and total mass ($F_{1,10} = 5.47, P < 0.05$), but larvae more strongly impacted U.S. plants than Chinese plants (Fig. 1). Both aboveground mass and total mass were not significantly different for U.S. and Chinese plants with larvae present, but U.S. plants were significantly larger than Chinese plants without larvae present (partial difference test, $P < 0.05$; Fig. 1). Interestingly, belowground mass was not significantly affected by either the interactions between plant origin and adults ($F_{1,10} = 2.06, P = 0.18$) or the interactions between plant origin and larvae ($F_{1,10} = 0.09$; partial difference tests, $P > 0.05$; Fig. 1).
1.35, \( P = 0.27 \)). In addition, there were not any significant interactions between adults, larvae, and origin in terms of plant mass (Appendix B).

Leaf area removed by adults depended on plant origin (\( F_{1,10} = 22.93, P < 0.0001 \)) and larval presence (\( F_{1,48} = 29.89, P < 0.0001 \)) but not their interaction (\( F_{1,10} = 0.17, P = 0.69 \); see Appendix C for full ANOVA table of herbivore response variables). The mean percentage of leaf area removed by adults was significantly higher for U.S. plants compared to Chinese plants (Fig. 2A). The U.S. plants had higher tolerance to aboveground damage as indicated by significantly steeper negative slopes for Chinese plants for aboveground mass (\( F_{1,10} = 7.83, P < 0.05 \)) and total mass (\( F_{1,10} = 5.87, P < 0.05 \)) vs. leaf area removed in regressions (Fig. 3A, C; see Appendix D for full slope, intercept, and test results). In contrast, the slopes for regressions of mass vs. belowground herbivory (number of larvae emerging as adults) were not significantly different between Chinese and U.S. plants (belowground, \( F_{1,10} = 0.30, P = 0.59 \); aboveground, \( F_{1,10} = 1.94, P = 0.19 \); total, \( F_{1,10} = 1.35, P = 0.27 \); Fig. 3B, D).

The survival of adults and larvae each depended on the presence of the other life stage. Larval survival to emergence increased when adults were present compared to when no adults were present (\( F_{1,48} = 24.21, P < 0.0001 \); Fig. 2B). This positive effect of adults on larvae was significantly higher for U.S. plants than those on Chinese plants (larval, \( F_{1,10} = 6.96, P < 0.05 \); adults, \( F_{1,10} = 4.67, P < 0.05 \); Fig. 2B, C).

**Discussion**

Invasive plants may employ novel defense strategies to cope with differing above- and belowground herbivore communities, thus potentially affecting above- and belowground feedbacks (van der Putten et al. 2009). Our experiments with tallow and the above- and belowground interaction between life stages of *B. collaris* illustrate this potential. To our knowledge, this study is the first to report how above- and belowground herbivory interact at both evolutionary and ecological scales to determine plant performance.

The better performance of aboveground feeding adults (leaf area removed and survival) on U.S. plants than on Chinese plants indicates that U.S. plants had significantly lower resistance than Chinese plants to aboveground herbivory. This result was not surprising as other studies have found such differences in resistance to aboveground chewing insect herbivores (Bossdorf et al. 2005). But the finding that there were significant differences in belowground resistance (higher larval survival on U.S. than on Chinese plants when adults were present) provides the first evidence supporting EICA for belowground herbivores. We acknowledge that there was no significant difference in belowground resistance between plant origins when only larvae were present. However, simultaneous herbivory by both adults and larvae may be more common than only...
larval herbivory, as *B. collaris* is multivoltine, above- and belowground herbivory often overlap in nature, and *B. collaris* overwinters as an adult. It may be that flea beetles are an unusual group for the study of above- and belowground interactions as some above- and belowground herbivore species occur in sequence and do not attack plants at the same time under natural conditions. Thus the interactions between above- and belowground herbivory of a single multivoltine species may differ from the interactions between two different above- and belowground species. A recent study indicated that interaction between above- and belowground herbivores of different species was dependent upon the sequence of arrival and early arrival may be an important strategy of herbivores to avoid competition with other herbivores and increase their performance (Erb et al. 2011). Moreover, population dynamics of a single species with above- and belowground stages differs from the population dynamics of two different species. However, flea beetles are common in nature and often successfully used for the biological control of invasive plants (Fornasari 1993, Julien and Griffiths 1998).

Aboveground herbivores had greater impacts on Chinese plants but belowground herbivores more strongly impacted U.S. plants, suggesting a role for herbivore tolerance. The higher aboveground tolerance of U.S. plants was more than sufficient to offset the effects of lower resistance to aboveground herbivory,
which was consistent with previous studies (Rogers and Siemann 2004, 2005, Zou et al. 2008, Huang et al. 2010, Wang et al. 2011). Increased aboveground herbivore tolerance may favor plant adaptation to variable environmental stresses, such as cutting or damage from fire, allowing the invasive plant to be more competitive with native plant species.

The negative effects of larvae on adults in this study might be due to asymmetrically induced systemic resistance to above- and belowground herbivores (Kaplan et al. 2008, van Dam 2009). But the most striking results were the strong positive effect of adult presence on larval survival to emergence and the stronger effect of adults with U.S. plants than with Chinese plants. This suggests that aboveground feeding of adults may be associated with lower defenses belowground and/or greater resources belowground, especially for U.S. plants. There is some evidence that plants may preferentially allocate their defenses to the shoot when both above- and belowground herbivores are present (Bezemer et al. 2004, Rasmann and Turlings 2007). Such a reallocation pattern may be adaptive from the perspective of the plant if there are greater negative effects of aboveground herbivores. In the current study, we found that the negative effect of aboveground herbivory on plant mass was significantly greater than that of belowground herbivory (means contrast results for larvae × adults). There is evidence in the literature for resource reallocation effects as well. For example, Kaplan et al. (2008) demonstrated that aboveground herbivory induced a putative tolerance response whereby aboveground nutritional reserves were allocated belowground, which in turn facilitated root-knot nematode performance.

Assuming that the number of larvae emerging as adults is correlated with the amount of belowground damage, our results indicate that the presence of adults increased the amount of damage from larvae. If so, the greater than additive effect of feeding by adults and larvae on plant mass appears to be partly the consequence of increased damage when both were present. This pattern of aboveground herbivory benefiting belowground herbivores is contrary to most theory and the general trend of aboveground herbivores negatively impacting belowground herbivores (Moran and Whitham 1990, Masters et al. 1993, Soler et al.
The impact of plant origin on those feedbacks, at least the stronger positive effect of aboveground adults on belowground larval survival, indicates that the differences in defense in U.S. vs. Chinese plants not only affect herbivore population dynamics, but also drive above- and belowground herbivore interactions. Our previous study found a specialist weevil, *Heterapoderopsis bicallosicollis* (both adult and larva feeding aboveground), built up larger populations on U.S. plants than on Chinese plants across four generations due to their lower resistance (Wang et al. 2011). For the specialist flea beetle *B. collaris* in this study, we observed its population for only one generation. Monitoring multiple generations may increase our understanding of above- and belowground herbivore feedbacks, especially differences driven by plant invasions.

Belowground feedbacks have received little attention in the context of plant–herbivore interactions in invasion biology (van der Putten et al. 2009, Kardol and Wardle 2010). The results in this study, however, clearly show that escape from belowground specialist herbivory improves invasive plant performance. When no belowground specialists were present, U.S. plants grew larger than Chinese plants, while they performed similarly to natives when attacked by belowground larvae. Thus, possibly due to decreased belowground allocation of U.S. plants, belowground herbivory more negatively affected U.S. than Chinese plants.

Overall, relative to plants from the native populations, plants from invasive populations had greater total and aboveground biomass, higher aboveground tolerance, and lower above- and belowground resistance. These results indicate that invasive tallow populations may adopt an “aboveground first” strategy in which the invader allocates resources aboveground, which not only increases tallow’s competitive ability for resources such as light but also enhances its ability to tolerate aboveground herbivory. To date, most studies of resource allocation in invasive plants have investigated the trade-offs between defense and growth (Joshi and Vrieling 2005, Franks et al. 2008, Huang et al. 2010, but see Oduor et al. 2011), but few have addressed how invasive plants allocate resource between above- and belowground to benefit their invasion success. Our findings may give insights into plant strategies in the context of above- and belowground defense and growth. In this study, the strategy of lower herbivore resistance and higher aboveground herbivore tolerance associated with plants from the invasive range was much more successful than the higher resistance and lower aboveground tolerance strategy of plants from the native range. Furthermore, the stronger positive effect of aboveground adults on belowground larval survival with U.S. plants than Chinese plants and lower root shoot of U.S. plants together with a general negative effect of larval feeding on adult survival suggest a preexisting emphasis on aboveground vs. belowground growth has been strengthened in the introduced range. This could reflect more intense aboveground herbivory by generalists than belowground generalists or greater importance of aboveground competition in the introduced range, relative to those in native range. We do not know whether the potential of enemy release from belowground herbivores to drive invasions is generally stronger than the release from aboveground herbivores for exotic plants, although greater success with belowground vs. aboveground biocontrol agents suggest it may be the case (Blossey and Hunt-Joshi 2003).

Our results may also have practical implications for biological control of invasive plants. Belowground biocontrol agents that feed on plants across life stages appear to have the potential to be especially damaging (Blossey and Hunt-Joshi 2003, van der Putten et al. 2005). Since invasive populations of tallow have increased tolerance to aboveground herbivores, release of biocontrol insects only feeding aboveground may have limited impact on the plant. In contrast, belowground feeding biocontrol insects may have a greater impact as the tolerance to belowground herbivory is not increased in invasive populations. Release of both above- and belowground insect agents or a single agent with above- and belowground stages may achieve a significant joint effect that neither could achieve alone. In addition to *B. collaris*, currently two more insect agents including the Noctuid caterpillar *Gadirha inexacta* (only larvae feed on leaves) and a leaf-rolling weevil *H. bicallosicollis* (both larvae and adults feed on leaves) are under evaluation for potential biological control of tallow in the United States. We predict that *B. collaris* will show greater impact on plant growth than these two insects due to both above- and belowground herbivory. Importantly though, evolved differences in herbivore resistance and tolerance could reduce the ability of biocontrol agents to successfully control target plants, and pre-release studies should include plant populations from the introduced range to more effectively predict the impact of agents. In the case of tallow, there appear to be differences in the ability of above- and belowground herbivory to impact plant growth. Screening and testing agents with only plants from the native range would overestimate the effectiveness of biocontrol agents.

In conclusion, this study shows that invasive plants such as tallow have evolved different responses to above- and belowground herbivory compared with their native populations. They may employ novel mechanisms for resource allocation among above- and belowground defenses and growth to cope with the differing above- and belowground herbivore communities. These are critical to understanding the linkages between above- and belowground processes that may further underlie invasion mechanisms. On a practical
level, our results indicate that knowledge of above- and belowground defense in invasive plants may improve the effectiveness of biological control.

Acknowledgments

We thank Anurag Agrawal, Ragan Callaway, Keith Clay, Nicole van Dam, and Yi Wang for comments and discussions, and Wei Hui for field assistance. We are grateful for comments by two anonymous reviewers that improved the early version of this manuscript. This study was supported by the China National Basic Study Program (2012CB11410) and the 100 Talent Program of the Chinese Academy of Sciences (to J. Ding), the U.S. National Science Foundation (DEB 0820560 to E. Siemann), an NSF pre-doctoral fellowship (to J. Carrillo), a Ford Foundation fellowship (to J. Carrillo), and the foreign visiting professorship of the Chinese Academy of Sciences (to E. Siemann).

Literature Cited


plants from America are better competitors and defenders. Ecological Monographs 78:369–386.


Zheng, H., Y. Wu, J. Ding, D. Binion, W. Fu, and R. Reardon. 2005. Invasive plants established in the United States that are found in Asia and their associated natural enemies. Forest Health Technology Enterprise Team, Morgantown, West Virginia, USA.


SUPPLEMENTAL MATERIAL

Appendix A
Geographical locations of Triadica sebifera populations from the native (Chinese) and invasive (U.S.) ranges that were used in this study (Ecological Archives E093-221-A1).

Appendix B
Full ANOVA results for plant response variables (Ecological Archives E093-221-A2).

Appendix C
Full ANOVA results for herbivore response variables (Ecological Archives E093-221-A3).

Appendix D
Full results of plant tolerance regressions (Ecological Archives E093-221-A4).