

Repeated damage by specialist insects suppresses the growth of a high tolerance invasive tree

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Abstract Many invasive plant species have high tolerance to herbivore damage, which can lead to low impacts of introduced biological control insects. High herbivore tolerance may be a trait acquired by invasive plants in their invaded range which makes it difficult to predict impacts of introduced insects. In this study, we compared the growth and foliar secondary chemical responses of invasive and native populations of *Triadica sebifera* (Chinese tallow tree) to repeated damage by specialist or generalist herbivores. We found repeated damage significantly decreased plant biomass and increased foliar tannin and flavonoid concentrations compared to a single damage event. These effects were significantly stronger with specialist damage than with generalist damage but the magnitudes of these differences were small. Plants

from invasive populations had lower foliar tannins and higher foliar flavonoids than plants from native populations and had greater biomass in every damage treatment. Our results suggest that repeated damage could suppress the growth of invasive plants with high tolerance. Thus using multivoltine herbivores as biological control agents may overcome herbivore tolerance and increase biological control efficacy.

Keywords Plant–insect interactions · Chemical ecology · Plant defense · Forest invasive plants · Biological control

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Introduction

Understanding the interactions between invasive plants and their herbivores is crucial for biological control of invasive plants. Introduction of host-specific natural enemies from the native range has been

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regarded as one of the promising approaches to controlling invasive plants worldwide for more than 100 years (Julien and Griffiths 1998; McFadyen 1998). Although many invasive plants have been suppressed by introduced insects, the overall biological control success rate is not high (McFadyen 1998). Many introduced insects establish populations on their target invasive plant but their impact is not sufficient to curb the invasion.

Though many biotic and abiotic factors have been implicated in the failure or low impact of biological control agents, plant tolerance to herbivory is potentially very important but only recently regarded as one of them (McFadyen 1998). Evolved increased tolerance due to changes in the growth rates of invasive plants may be a common phenomenon. Thus, to increase biological control success, it is critical to overcome plant tolerance (Milbrath 2008; Striker et al. 2011).

Tolerance is defined as the ability of a plant to maintain growth and fitness despite tissue damage (Weis et al. 2000) and is often measured as compensatory capacity after damage (Rosenthal and Kotanen 1994). This regrowth ability depends largely on its ability to re-establish leaves and renew photosynthesis because plants often do not maintain large stores of energy and nutrients and they need carbohydrates gained from photosynthesis to regrow (Olson and Richards 1988). Repeated damage could effectively suppress plant tolerance through removal of more leaves and meristems which are crucial for regrowth. Examples of repeated artificial defoliation being required to impact invasive plant performance include the invasive liana, *Macfadyena unguis-cati* (Raghu et al. 2006), the invasive vine *Vincetoxicum* sp. in high light conditions (Milbrath 2008), and the forage legume, *Lotus tenuis* (Striker et al. 2011). After repeated damage, plants may also need to reallocate resources to produce more resistance chemicals which may further decrease the resources available for growth (Underwood 2012).

For high tolerance invasive plants, repeated damage by some biological control agents, if they have more than one generation per year, could enhance the impact of herbivory and counter plant tolerance. However, impact studies in biological control programs frequently only evaluate the effect of damage within a single insect generation (Smith 2005; Gerber et al. 2008; Huang et al. 2011), possibly underestimating the potential of the herbivore to control its host plant. Previous studies have found that, for some

invasive plants, plants from introduced populations are able to tolerate herbivore damage better than those from native ones (e.g. Meyer et al. 2005; Ridenour et al. 2008; Huang et al. 2010; Wang et al. 2011) though other species do not have such variation in tolerance (e.g. van Kleunen and Schmid 2003; Bossdorf et al. 2004). It is not known whether invasive plants from introduced populations also have high tolerance to repeated damage which is critical for predicting the impact of multivoltine herbivores if they are considered as biological control agents. In addition, repeated damage could also change plant chemical resistance that may affect the insect community on invasive plants which could in turn impact biological control insects (Wang et al. 2011).

Here, we examine the impact of repeated damage by generalist and specialist herbivores on growth and defense of Chinese tallow tree *Triadica sebifera* (L.) Small [= *Sapium sebiferum* (L.) Roxb.]. Previous studies have reported that invasive *T. sebifera* have increased tolerance to a single episode of damage which limits herbivore impacts on plant growth (Rogers and Siemann 2003, 2004, 2005; Zou et al. 2008a, b, 2009; Wang et al. 2012b). Such damage also induces chemicals such as tannins and flavonoids (Wang et al. 2012a). In this study we use specialist and generalist insect to damage plants once, twice or three times to simulate the natural damage by multivoltine insects in the field. We focus on the impact of repeated damage and expect that such repeated damage by multivoltine biological control agents could decrease the plant tolerance. Specially, we asked the following questions: (i) Does repeated herbivore damage have larger impacts on plant growth than single damage? (ii) How do foliar flavonoid and tannin concentrations respond to repeated herbivore damage? (iii) Do generalist and specialist herbivores have similar effects on plant growth and chemical defenses? (iv) Do plants from the invasive and native ranges (continental origin) differ in their growth and defense responses to repeated damage by specialist and generalist herbivores?

Materials and methods

Study organisms

Native to Asia, *Triadica sebifera* is a common perennial tree (Zhang and Lin 1994). It was first

introduced to Georgia, USA in the late Eighteenth century for agricultural and ornamental purposes (Bruce et al. 1997) but has since become a noxious invasive weed in Florida, Louisiana, Mississippi, and Texas, USA (USDA/NRCS 2016). *T. sebifera* displaces native plants in grasslands, wetlands, and forests and forms monospecific stands (Bruce et al. 1997). It has the potential of spreading 500 km northward beyond current invaded areas (Pattison and Mack 2008) and to increase in abundance in many southern forests (Wang et al. 2011). We tested seedlings in our study because the seedling stage may play an important role in its invasion success (Bruce et al. 1997).

Previous studies suggest that *T. sebifera* has evolved to be a faster-growing and less herbivore-resistant plant in response to low herbivore loads in its invaded range (Siemann and Rogers 2003a,b; Siemann et al. 2006). Studies in the invaded range indicated that invasive populations of *T. sebifera* tolerate artificial and generalist damage more effectively relative to native populations (Rogers and Siemann 2003, 2004, 2005). In the native range, we also found that specialist herbivores perform better on invasive populations but invasive populations have stronger tolerance to specialist herbivores than native populations in common garden experiments (Wang et al. 2011). However, the impact of repeated damage on *T. sebifera* growth and resistance has not been tested so far.

Gadirtha inexacta Walker (Lepidoptera: Noctuidae) is a specialist insect feeding on *T. sebifera*, and it is potentially a biocontrol agent against *T. sebifera* (Wang et al. 2012b). The moth has four or five generations per year in Hubei province, China. The eggs of the moth overwinter on branches and leaves and hatch in May. Larvae feed on leaves, pass through six instars in approximately 15 days at 26 °C in the laboratory (Wang et al. 2012b). Larvae can cause severe damage, especially during the last three instars (Wang et al. 2012b).

Cnidocampa flavescens Walker (Lepidoptera: Limacodidae), a generalist defoliator, can also cause serious damage to *T. sebifera*. The moth has two to three generations per year in Hubei, overwintering as a mature larva in the cocoon. The larva pupate in mid-May and the adults appear in late-May. The neonate larvae feed on the lower leaf cuticle, producing small transparent circular patches. Feeding by late instars

produces large holes on the leaves. The larvae pass through seven instars in about 30 days at 26 °C in the laboratory (Wang et al. 2012b).

Seeds and seedlings

The experiments were conducted at Wuhan Botanical Garden, China in 2010. In late November 2009 we collected seeds from eight populations across south China (hereafter referred to as native populations) and eight populations from the southeast USA (hereafter referred to as introduced populations, see Supplementary Table S1). Molecular studies indicated that populations in the invaded range come from at least two distinct introduction events. The original introductions to Georgia and South Carolina were likely from a southern China population. Later introductions to the USA were likely from the northeastern part of *T. sebifera*'s range (DeWalt et al. 2011). Therefore, we consider the populations used in this experiment to be representative of the genetic variation in the native and introduced range.

For each population, seeds were collected from four to ten haphazardly selected *T. sebifera* trees. To evaluate the potential impacts of seed provisioning on seedling performance, 20 seeds from each population were weighed. Seed weights did not differ significantly between native and introduced populations (nested ANOVA, population was nested within continent, $F_{1,14} = 1.652$, $P = 0.246$). Therefore we can be confident that the observed differences in plant performance can be attributed to the impacts of herbivory. We removed the seed's waxy coats by soaking in water with laundry detergent (10 gl^{-1} Diaopai laundry detergent, Wuhan, China) for two days. Then we buried the seeds in sand at a depth of 5–10 cm and placed them in a refrigerator (4 °C) for 40 days.

Experimental design

On April 15 2010, seeds of the 16 populations were planted and maintained in a greenhouse for six weeks. Similar-sized healthy seedlings were selected on June 20 2010 and transplanted individually into pots (height: 16 cm, diameter: 25 cm) containing growing medium (50 % locally collected field soil and 50 % sphagnum peat moss) and placed in an outdoor common garden. Each plant was enclosed by a nylon mesh cage (100 cm height; 27 cm diameter) to exclude herbivores.

Seedlings were randomly assigned to one of seven different treatments in a factorial design with two factors (herbivore type [generalist or specialist] and damage frequency [1, 2, or 3]) plus undamaged controls. In total there were 560 seedlings ($[8 + 8] \times [2 \times 3 + 1] \times 5$ replicates).

On 16 July, three to five third-instar larvae of *G. inexacta* or *C. flavescens* were released into cages with seedlings assigned to an herbivore treatment (G1, G2 or G3 for damage by the generalist *C. flavescens* once, twice and three times, respectively; S1, S2 or S3 for damage by the specialist *G. inexacta* once, twice and three times respectively). The survival of larvae was monitored and those that died during the course of the experiment were replaced with the corresponding larval stage. When larvae had eaten all leaves of the seedling (100 % damage), they were removed. On 14 August, larvae were added for the second damage event (G2, G3, S2, or S3) and on 12 September, larvae were added for the third damage event (G3 or S3). On 25 October, we harvested all plants (including leaf, stem and root) which were oven dried to a constant weight at 40 °C for five days to determine their dry biomass. The dried leaves were used for chemical analyses.

Chemical analyses—flavonoids and tannins

We measured five flavonoids (quercetin, isoquercetin, quercetin glycoside, kaempferitrin and kaempferol) with high performance liquid chromatography (HPLC) following (Wang et al. 2012a). We purchased quercetin, isoquercetin, and kaempferol standards from Sigma-Aldrich (St. Louis, MO, USA) and obtained quercetin glycoside and kaempferitrin standards from the National Institutes of Food and Drug Control (Beijing, China). All standards had purity ≥ 97 % and were suitable for HPLC. We dried and ground leaves, then weighed them and soaked them for 24 h in a methanol: 0.4 % phosphoric acid in water solution (48:52, v:v). We filtered solutions through a 0.22 μm membrane. We injected filtered extract (20 μl) into a Dionex ultimate 3000 series HPLC (Dionex, Sunnyvale, CA, USA) with a ZORBAX Eclipse C18 column (4.6 \times 250 mm, 5 μm , Agilent, Santa Clara, CA, USA). We eluted flavonoids with a constant flow of 1.0 ml min^{-1} with a methanol: 0.4 % phosphoric acid in water gradient as follows: 0–10 min, 48:52 (v:v); 10–18.5 min, 65:35 (v:v). We

recorded UV absorbance at 254 nm. We used peak areas of standards of known concentrations to obtain percent dry mass for each of the five flavonoids. We calculated total flavonoid concentration, as percent dry mass, as the sum of these five concentrations.

We measured four tannins (gallic acid, catechin, tannic acid and ellagic acid) with HPLC following Wang et al. (2012a). We purchased standards suitable for HPLC (i.e. with a purity ≥ 95 %) from Sigma-Aldrich. We dried, ground, and weighed leaves then extracted them ultrasonically in a 50 % aqueous methanol solution for 30 min. We filtered the mixture through a 0.45 μm membrane and injected the extract (20 μl) into the same HPLC system described above. We eluted tannins at a constant flow of 1.0 ml min^{-1} with methanol: 0.1 % phosphoric acid in water gradient as follows: 0–7.5 min, 30:70 (v:v); 7.5–17 min, 55:45 (v:v). We measured UV absorbance at 279 nm for gallic acid, catechin, and tannic acid and at 260 nm for ellagic acid. We used peak areas of standards of known concentrations to obtain percent dry mass for each of the four tannins. We calculated total tannin concentration as percent dry mass as the sum of these four concentrations.

Statistical analysis

We used mixed model ANOVAs to examine the effects of plant origin (continent), damage frequency, herbivore type nested within damage frequency, and their interactions on chemical concentrations and plant biomass. We treated population nested within origin as a random effect. We used population (origin) as the error term to test for a significant effect of origin. We included herbivore type as a nested term in order to include the undamaged controls in the analyses. Because the contrast between no damage and damaged is fitted by the damage frequency term, the nested herbivore term corresponds to herbivore identity within a damage frequency. This approach does not allow the fitting of a separate herbivore type by damage frequency term but in reduced models that excluded undamaged controls this term was only significant for biomass (see Supplementary Table S2). We used adjusted means partial difference tests to examine whether treatments differed for predictors with more than two levels. All data analyses were performed with the statistical analysis software SAS, ver. 9.1 (SAS Institute Inc. USA).

Table 1 The influence of continental origin of *Triadica sebifera* tree populations [Cont], damage frequency [Dam], herbivore type nested in damage frequency [Herb (dam)], and

their interactions on plant biomass, leaf tannins and flavonoids concentrations in a mixed model ANOVA

Effect	Df	Biomass (g)		Tannins (% dw)		Flavonoids (% dw)	
		F	P	F	P	F	P
Cont	1,14	6.97	0.0194	4.72	0.0475	1.05	0.3219
Dam	3,532	148.80	<0.0001	110.26	<0.0001	69.94	<0.0001
Herb(dam)	3,532	6.88	0.0001	10.25	<0.0001	7.19	<0.0001
Cont×dam	3,42	1.06	0.3746	5.91	0.0019	2.67	0.0594
Cont×herb(dam)	3,42	4.98	0.0048	2.63	0.0623	0.44	0.7240

Significant results are shown in bold

Results

Impact of repeated damage on plant biomass

For invasive populations, plant biomass decreased with damage frequency for both the specialist and generalist herbivore and biomass was lower with specialist feeding than with generalist feeding when damage frequency was one or three (Table 1; Fig. 1). For native populations, biomass decreased with all types of herbivore damage except when damage frequency was one by the specialist (Table 1; Fig. 1). For damage frequency two, biomass was lower with specialist feeding compared to generalist feeding but the two herbivores had similar impacts at one or three feedings (Fig. 1). For damage by the specialist, plant biomass was lower when damage frequency was greater than one, while plant biomass for damage frequency three was lower than that for lower damage frequencies for damage by the generalist (Fig. 1). Plants from invasive populations were larger than those from native populations in every damage treatment (Fig. 1).

Impact of repeated damage on leaf chemicals

Specialist herbivore damage induced more tannins and flavonoids than generalist herbivore damage (Table 1; Fig. 2a,c, see Supplementary Table S2, Fig. S1). Invasive populations had lower foliar tannin concentrations than native populations at every damage frequency but concentrations were comparable in the absence of damage (Table 1; Fig. 2b). Repeated damage significantly increased foliar tannins for both invasive and native populations but

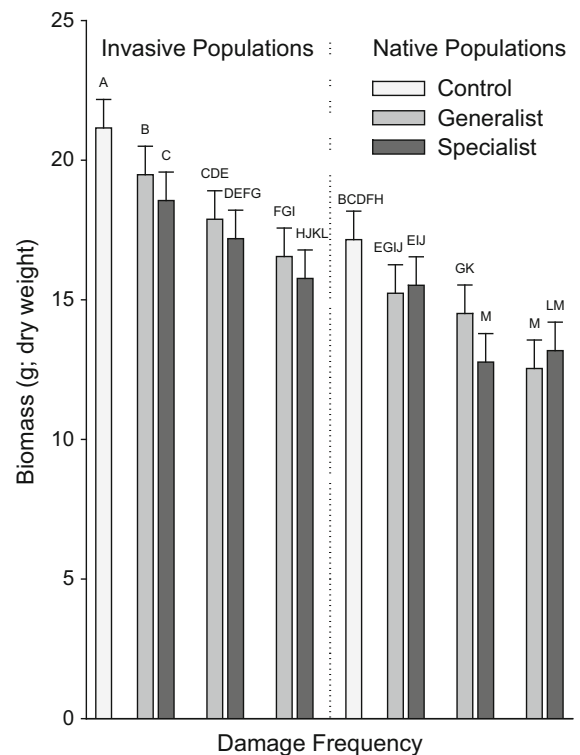


Fig. 1 Average (+SE) effect of damage frequency (0, 1, 2 or 3 times) by a generalist (*Cnidocampa flavescens*) or specialist herbivore (*Gadirtha inexacta*) on plant biomass of invasive and native *Triadica sebifera* populations. Each herbivore feeding represents 100 % leaf damage. Bars with shared letters indicate means that were not significantly different in post-hoc tests in the nested model that included controls ($P \geq 0.05$)

plants from invasive populations increased tannins more gradually with damage than ones from native populations did (Table 1; Fig. 2b). Flavonoid concentrations were comparable for undamaged plants

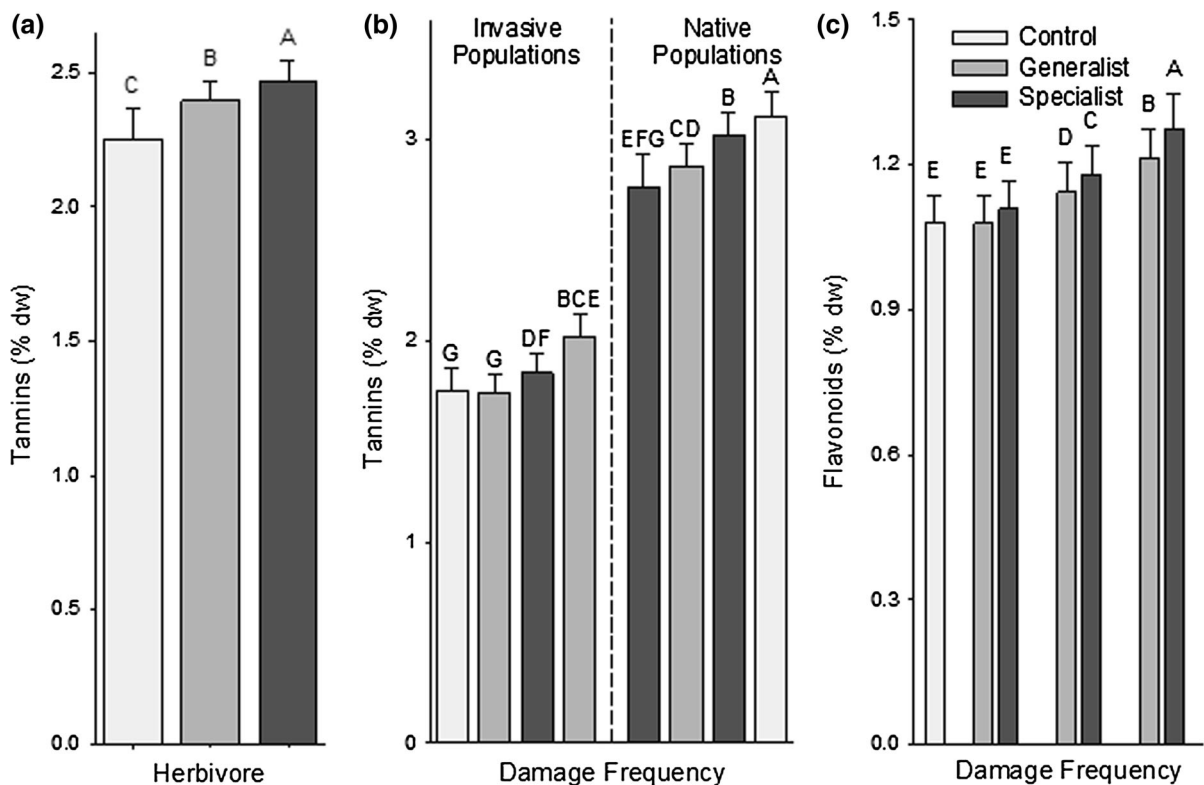


Fig. 2 Average (+SE) effect of (a) damage and (b) number of times damaged (0, 1, 2 or 3 times) by a generalist (*Cnidocampa flavescens*) or specialist herbivore (*Gadirtha inexacta*) on invasive and native *Triadica sebifera* foliar tannin and (c) foliar

flavonoid concentrations. The units for foliar chemical concentrations are % dry weight (dw). Bars with shared letters indicate means that were not significantly different in post-hoc tests in the nested model that included controls ($P \geq 0.05$)

and plants damaged a single time but they increased with higher damage frequency, with the concentrations significantly higher with more damage events and for specialist feeding compared to generalist feeding (Table 1; Fig. 2b).

Discussion

We found repeated damage significantly decreased plant biomass and increased foliar tannin and flavonoid concentrations compared to a single damage event. These effects were significantly stronger with specialist damage than with generalist damage but the magnitudes of these differences were small. Plants from invasive populations had lower foliar tannins and higher foliar flavonoids than plants from native populations and had greater biomass in every damage treatment.

Previous studies have reported that, relative to native populations, invasive *T. sebifera* populations have increased tolerance to damage which will limit the herbivore's impact on plant growth under single damage (Rogers and Siemann 2003, 2004, 2005; Zou et al. 2008a, b, 2009; Wang et al. 2012b). Invasive tallow populations are able to maintain higher growth and fitness after damage and often have stronger compensatory capacity than native populations (Rogers and Siemann 2005). For some other invasive plants, plants from introduced populations were also reported to have higher tolerance to herbivore damage than those from native ones (e.g. Meyer et al. 2005; Ridenour et al. 2008). Although *T. sebifera* could regrow quickly even after serious damage such as 100 % leaf area being removed (Wang et al. 2012b), this regrowth ability is also limited by energy and nutrients because they need carbohydrates gained from photosynthesis to regrow (Olson et al. 1997). Previous studies have found that

repeated damage could effectively suppress plant tolerance through removal more leaves and meristems which are crucial for regrowth (Raghu et al. 2006; Milbrath 2008).

Repeated damage is expected to remove more leaves and meristems than single damage, because after repeated damage, plants need to restructure more new leaves to get enough nutrients and also need to reallocate resources to produce more resistance chemicals to defend against herbivores. Thus, multiple damage may induce high concentration of defense chemicals (Underwood 2012) which may further decrease the resources available for growth, because of resource trade-offs between defense and growth (see reviews by Stamp 2003 and Koricheva et al. 2004). It is possible, however, that such increases in defense chemicals could reduce the amount of damage from subsequent herbivore feeding events. In this study we found repeated damage by herbivores could significantly increase the concentration of tannins and flavonoids in leaves. To respond to repeated damage, *T. sebifera* might reallocate more resources to chemical resistance, resulting in reduced growth. The cost of constitutive and herbivore-induced chemical defenses has been reported for invasive plants (Zas et al. 2011; Sampedro et al. 2011), especially in low resource availability conditions. So in some resource limited habitats, repeated damage could have higher impact on the growth of invasive plants.

Resource availability (light, water, nutrients, etc.) that influences the growth and tolerance of invasive plant species (Dukes and Mooney 1999; Davis et al. 2000; Rogers and Siemann 2003) may affect the outcome of biological control (Blumenthal et al. 2009). From previous studies we found that invasive *T. sebifera* populations have higher tolerance to herbivores than native populations under light and shade conditions (Wang et al. 2011) but when damaged several times under low light levels, they regrew slowly and their mortality significantly increased (Wang et al. 2012a, b). Thus in some conditions of low resource availability, repeated damage could have a greater impact on invasive plants, likely decreasing their competitive advantage over native forest species.

Our findings have very important implications for management of invasive plants. Weed biological control programs can fail because introduced biological control agents may not suppress the regrowth of invasive plants that have high tolerance to herbivory.

Introduced herbivores may become abundant but not effectively suppress target weeds, some of which could also lead to direct and indirect non-target effects (Pearson and Callaway 2003). However, repeated defoliations could effectively suppress target weeds, and reduce the risk of non-target effects. In addition, our results suggest that augmentative biological control, i.e., periodically releasing natural enemies to control target pests (Bale et al. 2008; van Lenteren and Bueno 2003), may be an effective way to control invasive plants with high tolerance. In conclusion, repeated damage by multiple releases of the same insects or by release of multivoltine herbivores may decrease the invasive plant tolerance and improve control efficacy.

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