

Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant

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Summary

1. Invasive plants often have novel biotic interactions in their introduced ranges. These interactions, including less frequent herbivore attacks, may convey a competitive advantage over native plants. Invasive plants may vary in defence strategies (resistance vs. tolerance) or in response to the type of herbivore (generalists vs. specialists), but no study to date has examined this broad set of traits simultaneously.

2. Here, we examined resistance and tolerance of Chinese tallow (*Triadica sebifera*) populations from the introduced and native ranges to generalist (*Cnidocampa flavescens*) and specialist herbivores (*Gadirtha inexacta*) in the native range.

3. In a field common-garden test of resistance, caterpillars of each species were raised on plants from native and invasive populations. We found the specialist grew larger on and consumed more mass of invasive plant populations than native populations, while the generalist showed the same performance between them. The results were consistent with our laboratory bioassay using excised leaves. Chemical analyses showed that the invasive plants had lower tannin content and higher ratio of carbohydrate to protein than those of their native counterparts, suggesting that plants from invasive populations have altered chemistry that has a larger impact on specialist than on generalist resistance.

4. To test for differences in herbivore tolerance, plants were first defoliated by specialist or generalist herbivory and then allowed to regrow for 100 days in a field common garden. We found that plants from invasive populations had greater herbivore tolerance than native populations, especially for tolerance to generalists. They also grew more rapidly than native counterparts in the absence of herbivory.

5. Synthesis. The results of these experiments indicate that differences in selective pressures between ranges have caused dramatic reductions in resistance to specialist herbivores and those changes in plant secondary chemistry likely underlie these differences. The greater tolerance of invasive populations to herbivory appears to at least partly reflect an increase in growth rate in the introduced range. The greater tolerance to generalist herbivores suggests the intriguing possibility of selection for traits that allow plants to tolerate generalist herbivores more than specialist herbivores.

Key-words: biological control, Chinese tallow, *Cnidocampa flavescens*, evolution of increased competitive ability, *Gadirtha inexacta*, invasion ecology, resistance, tolerance

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Introduction

Understanding the mechanisms underlying biological invasions is crucial for managing invasive species (Williamson 1996; Mack *et al.* 2000; Davis 2009). In the context of biotic interactions, several hypotheses have been proposed to explain the invasion success of some exotic plants (see Mitchell *et al.* 2006 and references therein). The 'enemy release' hypothesis proposes that exotic plants explode in abundance through escaping suppression from natural enemies in their native range (Elton 1958; Maron & Vilà 2001). Blossey & Nötzold (1995) predicted that release from natural enemies allows exotic plants to reallocate their resources from defence against natural enemies to growth and reproduction, thus evolving increased competitive ability in their introduced range (EICA hypothesis). Although numerous studies have recently examined these hypotheses, we still have no general conceptual framework for the role biotic interactions play in invasions, and the debate over the relative importance of various factors and the interactions among them is still intensive (Bossdorf *et al.* 2005). For instance, there are trade-offs between resistance to specialists vs. generalists as well as between herbivore resistance vs. herbivore tolerance that may be critical for the success of invasive plants.

Both the enemy release and the EICA hypotheses assume that introduced plants are primarily released from specialist herbivores (feeding on one or a few closely related plant species) (Keane & Crawley 2002); however, the impacts of generalists (feeding on multiple non-related plant species) on plant invasion are largely neglected (but see Maron & Vilà 2001; Agrawal & Kotanen 2003; Lankau, Rogers & Siemann 2004; Parker & Hay 2005). Given that specialists and generalists may select for different defence mechanisms (van der Meijden 1996; Lankau 2007), studies addressing both simultaneously may be able to tease apart the effects of balancing multiple defence demands on invasion processes (Bossdorf *et al.* 2005).

Specialist and generalist herbivores can exert opposing selection pressures on chemical defence (Lankau 2007). High concentrations of plant toxins might deter generalists while attracting specialists that either use them as a cue to locate or to accept the host plant for oviposition and/or feeding (specialist-generalist dilemma) (van der Meijden 1996; Müller-Schärer, Schaffner & Steinger 2004). Specialists and generalists may also vary in their responses to quantitative defence compounds (e.g. tannins) that usually constrain the growth rate of the plant (Müller-Schärer, Schaffner & Steinger 2004). Based on the enemy release and the EICA hypotheses and specialist-generalist dilemma, Joshi & Vrieling (2005) predicted that plants introduced into areas where specialists are absent, but generalist herbivores readily feed on the introduced plant, may evolve increased resistance to generalists but decreased resistance to specialists. This prediction of reduced resistance to specialists and increased resistance to generalists was confirmed through a study in the *Senecio jacobaea* system (Joshi & Vrieling 2005). A number of studies have examined only a single type of herbivore and found a variety of patterns, including increased or decreased generalist or specialist resistance (Leger & Forister

2005; Stastny, Schaffner & Elle 2005; Caño *et al.* 2009). Other patterns have also been found, such as decreased resistance to generalists but no change in resistance to specialists (Hull-Sanders *et al.* 2007), decreased resistance to specialists but no change in resistance to generalists (Bossdorf *et al.* 2004), or increased resistance to generalists and specialists (Ridenour *et al.* 2008). Although no clear pattern has emerged, multidimensional trade-offs among plant defence strategies may explain some of this variation.

For example, plant defence against specialist and generalist herbivores may involve both resistance and tolerance strategies. Resistance is a plant trait that reduces the preference or performance of herbivores (Strauss *et al.* 2002), whereas tolerance is the ability of a plant to withstand and survive a fixed amount of herbivore damage without a corresponding reduction in fitness (McNaughton 1983; Paige & Whitham 1987; Strauss & Agrawal 1999). Trade-offs, i.e. negative correlations between resistance and tolerance to herbivory damage, have been reported in both agricultural and wild plants (see Leimu & Koricheva 2006 and references therein), including morning glory, *Ipomoea purpurea* (Fineblum & Rausher 1995). Such trade-offs between herbivore resistance and herbivore tolerance traits may be important for understanding the success of exotic plants.

Including tolerance as an herbivore defence strategy in a conceptual framework for biological invasions increases our ability to explain observed patterns. Selection for resistance can result in a correlated negative response in tolerance, and *vice versa*, whereas the costs of these defensive strategies may differ among environments and populations (Fornoni *et al.* 2004). Therefore, in the absence of specialist herbivores in the introduced range, reallocation away from herbivore resistance towards growth and reproduction may translate into increased tolerance to herbivores. Examining only variation in herbivore resistance but not herbivore tolerance may lead to spurious conclusions about the strength of top-down regulation by herbivores if there is a negative relationship between these two traits. Despite the fact that it may be critical to understand how populations of invasive plants vary in their response to type of herbivores (generalists vs. specialists) or in their responses to different herbivore defence strategies (resistance vs. tolerance), no study to date has examined this broad set of traits simultaneously.

We examined biogeographical variation in plant resistance and tolerance to herbivory by both specialist and generalist herbivores using Chinese tallow [*Triadica sebifera* (L.) Small = *Sapium sebiferum* (L.) Roxb., hereafter '*Triadica*'] as a model species. Previous studies suggest that *Triadica* has evolved to be a faster-growing and less herbivore-resistant plant in response to low herbivore loads in its introduced range (Siemann & Rogers 2001, 2003a,b; Siemann, Rogers & Dewalt 2006), providing evidence to support the EICA hypothesis. Recent studies also indicate that invasive populations of *Triadica* tolerate herbivory more effectively relative to native populations (Rogers & Siemann 2004, 2005; Siemann, Rogers & Dewalt 2006; Zou, Rogers & Siemann 2008; Zou *et al.* 2008). However, these patterns may depend on the type of herbivory

as well. To further understand *Triadica* invasion and defence mechanisms, there are still many critical issues to be solved in this system. For example, are there defence trade-offs between specialists and generalists, and does this depend on population origin (native vs. invasive), given that specialists are absent but generalists are present in the introduced range? Does decreased resistance to specialists translate into increased resistance or/and tolerance to generalists?

In this study, we conducted laboratory and field common-garden experiments to compare the resistance and tolerance of different *Triadica* populations to herbivory by native specialist and generalist caterpillars in China. We hypothesize that: (i) release from specialists in the invasive range favours increased defence to generalists; and (ii) decreased resistance to specialists favours increased tolerance and rapid plant growth. Specifically, we ask: (i) How do specialists and generalists vary in consumption and development rates when feeding on *Triadica*? Does plant origin (native vs. invasive range) affect herbivore performance? How do native and invasive populations of *Triadica* differ in nutrients and secondary chemical compounds? (ii) Does herbivory by specialists vs. generalists cause different compensatory responses by *Triadica*? Do native and invasive populations differ in their tolerance and growth?

Materials and methods

STUDY ORGANISMS

Triadica is a rapidly growing, polycarpic tree that typically starts to flower and set seeds after 3–8 years, although seeds can be produced by younger plants in the introduced range in ideal conditions (Grace 1998). It may grow to 10–13 m in height (Zhang & Lin 1994; Bruce *et al.* 1997). 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, both *Triadica* seedlings and adult trees have become severe invaders that aggressively displace native plants and form monospecific stands in the south-eastern USA (Bruce *et al.* 1997; Siemann & Rogers 2003c).

Gadirtha inexacta Walker (Lepidoptera: Noctuidae) is host-specific to *Triadica*, being considered as a potential biological control agent against *Triadica* (Y. Wang & J. Ding, unpubl. data). The eggs of the moth overwinter on branches and leaves and hatch in May. The larvae, which pass through six instars in about 15 days, feed on leaves and can cause severe damage, especially during the last three instars.

Cnidocampa flavescens Walker (Lepidoptera: Limacodidae), a generalist defoliator, can also cause serious damage to *Triadica*. The moth has two generations per year in the Hubei Province, China, and overwinters as mature larva in the cocoon. The larva pupates and the adult appears in mid- and late-May, respectively. The neonate larvae feed on the lower leaf cuticle and mesophyll, producing small transparent circular patches. The larvae pass through seven instars in about 30 days. Feeding by late instars produces large holes in the leaves.

We field-collected newly emerged adults or larvae of *G. inexacta* and *C. flavescens* from April to June 2008 and reared them on potted *Triadica* (Wuhan population) in the Wuhan Botanical Garden, at the Chinese Academy of Sciences, Hubei, China (30°32' N, 114°24' E). The offspring of these collections was used for experiments.

SEED AND SEEDLINGS

We conducted the experiments with the specialist and generalist caterpillars at Wuhan Botanical Garden in 2008. In late November 2007, we collected seeds from six populations across south China (hereafter referred to as native populations) and six populations from the south-eastern United States (referred to as invasive populations, Table 1). Previous genetic analysis suggests that Chinese tallow trees from Jiangsu Province, the northernmost province sampled, may be the source of non-Georgia and non-South Carolina US genotypes, while the Georgia and South Carolina genotypes may be derived from Guangdong Province in the south of China (Dewalt, Siemann & Rogers 2006; S. J. Dewalt, E. Siemann & W. E. Rogers, unpubl. data), as such we consider the populations used in this experiment to be representatively native and invasive.

For each population, seeds were collected from 4 to 10 haphazardly selected *Triadica* trees. To evaluate the potential impacts of seed provisioning on seedling performance, 20 seeds from each population were weighed. No difference was detected in seed weight of invasive and native populations ($F_{1,10} = 1.464$, $P = 0.254$, nested ANOVA). The seeds' waxy coats were removed by soaking in water with laundry detergent (10 g L^{-1}) for 2 days. The seeds were then buried in sand at a depth of 5–10 cm and placed in a refrigerator (4°C) for 35 days.

On 21 March 2008, seeds of 12 populations were planted and maintained in a greenhouse for 6 weeks. Similar-sized seedlings were selected for the experiments on 5 May 2008 and these were transplanted individually into pots (height: 16 cm, diameter: 25 cm) containing growing medium (50% field soil and 50% sphagnum peat moss) and arranged in an outdoor common garden. The seedlings were randomly assigned to either a common-garden or laboratory experiment. In the common-garden experiment, each plant was enclosed by a nylon cage (100 cm height; 27 cm diameter) to exclude herbivores. For the laboratory experiment, all plants were enclosed in a single $1.5 \times 10 \times 1.5 \text{ m}$ nylon cage.

LABORATORY EXPERIMENT

To test for differences in resistance of plants from the native and invasive range to herbivory by specialist (*G. inexacta*) and generalist (*C. flavescens*) insects, we conducted a laboratory experiment from August to September in 2008. We randomly assigned leaves of each population to either a specialist or generalist bioassay. We excised one fully expanded leaf (third or fourth position from the tip) from a plant of each population. Leaves were cut symmetrically along the mid-vein using scissors. We weighed each half and adjusted to the same weight to correct for mass differences in asymmetrical leaves. One leaf half was dried (80°C) for 2 days and weighed (Sartorius Balance, Readability: 0.0001 g) (i.e. leaf dry wt before feeding, hereafter 'LDW1'). The other leaf half was fed to a newly hatched larva on moist filter paper in a Petri dish (ID: 9 cm). Petri dishes were closed and incubated in the laboratory at 24°C and a 14/10 h (light/dark) photophase. To minimize error in estimating consumption, we replaced leaf halves with a fresh leaf half when 80% of the leaf was consumed. The uneaten leaf remains were then dried at 80°C for 2 days and weighed (i.e. leaf dry wt after feeding, hereafter 'LDW2'). We calculated dry wt of leaf mass consumed ($\sum \text{LDW1} - \sum \text{LDW2}$). The larvae were reared until pupation. During the experiment, we recorded the last instar larval fresh wt and larval development time. Each population (native or invasive) \times treatment (specialist or generalist) combination was replicated ten times.

Table 1. Location and historical presence for 15 populations of *Triadica* used (x) as seed sources in the laboratory experiments (examining resistance), common-garden experiments (examining both resistance and tolerance) and for chemical analysis of carbohydrate (C), protein (P) and tannins (T)

ID	Site of seed collection	Introduction year	Longitude	Latitude	Laboratory experiment	Common-garden experiment	Chemical analysis
Native	China						
KL	Guizhou	Native	26°32' N	108°04' E	x	x	x (T)
FJ	Fujian	Native	26°55'–27°26' N	119°55'–120°43' E	x	x	x (C, P, T)
AJ	Hunan	Native	27°18' N	110°06' E	x	x	x (C, P, T)
CD	Hunan	Native	29°12' N	111°37' E	x	x	x (T)
LT	Hubei	Native	31°06' N	115°43' E	x	x	x (C, P, T)
NJ	Jiangsu	Native	31°14' N	118°22' E	x	x	x (C, P, T)
GD	Guangdong	Native	24°46' N	112°22'–112°25' E			x (C, P, T)
SI	Sichuan	Native	29°20'–29°34' N	104°03'–104°46' E			x (C, P, T)
JN	Jiangsu	Native	32°22' N	119°26' E			x (C, P, T)
Invasive	USA						
GA	Georgia	1772	31°22'–32°05' N	81°06'–81°52' W	x	x	x (C, P, T)
SC	South Carolina	1772	32°15'–33°22' N	79°16'–80°76' W	x	x	x (C, P, T)
FL	Florida	c. 1865	29°89'–30°51' N	81°29'–87°23' W	x	x	x (C, P, T)
LA	Louisiana	c. 1900	31°15' N	91°33' W	x	x	x (C, P, T)
TX	Texas	c. 1900	29°22'–29°47' N	94°02'–94°46' W	x	x	x (C, P, T)
AL	Alabama	c. 1900	30°25' N	88°08'–88°13' W	x	x	x (C, P, T)

COMMON-GARDEN EXPERIMENT

To test for differences among native and invasive populations in response to herbivory by the specialist (*G. inexacta*) and generalist (*C. flavescentis*) in the field, we conducted a field common-garden experiment from May to November in 2008. The experiment was conducted separately (i.e. at slightly different times) for specialists and generalists since the two herbivore species were available at different times.

Generalist treatment

Ten similar-sized randomly selected plants from each population (native vs. invasive) were assigned to generalist herbivory treatments (herbivory vs. no herbivory control). Each treatment was replicated five times for each population. A single first instar of *C. flavescentis* was individually released into cages assigned to the herbivory treatment. We tested for differences in plant resistance among native and invasive populations by measuring defoliation of each seedling every day using a transparent grid with 1-mm² resolution. Ten days later, caterpillars were removed from seedlings and weighed. An additional 4–10 larvae were then added to obtain 100% defoliation. When the defoliation for each seedling reached 100% (about 10 days after those larvae were added), all insects were removed. To determine plant compensatory ability, the plants were allowed to regrow for 100 days. Plants were harvested on 22 October 2008, when we again measured plant height. The above- (leaf, shoot and stem) and below-ground (root) parts of the plants were then separated and dried at 80 °C for 48 h and weighed.

Specialist experiment

We followed the same protocol as above for the specialist *G. inexacta*, but the harvest was conducted on 20 November 2008, as in the field *G. inexacta* occurred about 1 month later than *C. flavescentis*.

The damage levels in our study reflect the levels that can be found in natural conditions in the native range. In the first stage of our field common-garden experiment examining resistance, the damage levels (10% leaf area removed by the generalist and 30–40% by the special-

ist) resemble damage reported in another study in the native range in which herbivores naturally recruited to plants (Zou, Rogers & Siemann 2008; Zou *et al.* 2008). Since heavy damage (>80% leaf area) has occasionally been observed in China (J. Ding, pers. obs.), complete defoliation is likely when insects outbreak. Thus, the 100% defoliation in the tolerance test may also happen in the invasive range, if the specialist moth is introduced into the US as a biological control agent.

CHEMICAL ANALYSIS

Primary compounds

Primary compounds involved in fundamental plant physiological processes may have profound effects on the behaviour and physiology of insects (Haukioja *et al.* 1991; Berenbaum 1995). To examine differences of primary compounds, i.e. proteins and carbohydrates, among native and invasive populations, we conducted chemical analysis using plants of 13 populations (seven native and six invasive populations, Table 1).

In March 2009, seeds were planted and maintained in a greenhouse for 6 weeks. Then seedlings were transplanted to five 1 × 25 m plots established at an open site in Wuhan Botanical Garden. Each plot contained 20 seedlings per population. No fertilizer or pesticides were added, but we added water as needed during the growing season. In October 2009, one pair of fully expanded leaves (third or fourth position from the tip) was collected from each of two undamaged seedlings per population and plot and placed in plastic vials, which were immediately transported to the laboratory in an insulated box filled with ice. The leaf material was weighed and ground in liquid nitrogen to a fine powder with a pre-chilled mortar and pestle. The leaf powder (100–300 mg fresh wt) was used for chemical analysis. Analysis of protein content was based on the method of Bradford (1976), using Bovine Serum Albumin (BSA) as the standard and absorbance determined by spectrophotometer at 595 nm. We determined carbohydrate colorimetrically by the anthrone–sulfuric acid method, reading absorbance at 630 nm by spectrophotometer (Dreywood 1946), report it as mg content per gram leaf fresh wt.

Secondary compounds

Many plants produce secondary chemical compounds, such as tannins, that are generally known to be a measurement of quantitative resistance against specialist herbivory. To determine whether there were underlying differences in plant quantitative resistance among native and invasive populations to herbivores, we conducted an analysis of tannin contents in plants of native and invasive populations. As plant ontogeny can affect the expression of resistance to herbivore damage as plants develop from seeds to seedlings, juveniles and mature stages (Boege & Marquis 2005), we included four different ages (years) of plants in our tests.

Seeds were planted and maintained in a greenhouse for 6 weeks beginning in April 2006 (one native population), April 2007 (one native and one invasive population) and March 2008 (six native and six invasive population) respectively. Then seedlings were transplanted to field plots established at an open site in Wuhan Botanical Garden. The seedlings were treated following the same protocol as above for primary compounds. All these seedlings, plus the seedlings sown in 2009, are hereafter referred to as 4-year-old seedlings (2006), 3-year-old seedlings (2007), 2-year-old seedlings (2008) and 1-year-old seedlings (2009). In October 2009, a pair of fully expanded leaves (third or fourth position from the tip) was collected from each undamaged seedling, dried and weighed and analysed for tannins. Total tannin contents were estimated by using a radial diffusion assay of tannin-mediated protein precipitation (Hagerman 1987). Leaf extract (20 µL) was placed in a 5-mm diameter hole, 1% (wt/vol) agarose plate with 0.1% (wt/vol) BSA. Plates were incubated at 30 °C and the area of precipitated proteins was measured with callipers after 96 h. Tannin concentrations were expressed as the amount of tannic acid standard needed to precipitate the same amount of protein on a per dry wt leaf mass basis.

STATISTICAL ANALYSES

To examine differences in resistance between native and invasive populations in the laboratory experiment, we performed mixed ANOVAS on the specialist or generalist larval development and feeding results. The models included continent (native vs. invasive) as the fixed effect and plant populations nested within continent as the random effect.

For the field common-garden experiment, mixed ANOVAS were performed on the specialist or generalist larval development and feeding results, as in the laboratory experiment. We tested differences in plant growth between native and invasive populations with mixed ANOVAS. The models included continent (native vs. invasive) and treatment (herbivory vs. control) as fixed effects, and plant populations were nested within continent as a random effect.

For the plant response to herbivory in the field common-garden experiment, a tolerance score was calculated as the ratio of the total biomass for damaged plants divided by the mean value of undamaged controls in the same herbivore treatment and population. This corresponds to the slope of the reaction norm for the invasive or native populations across herbivore treatments (herbivores present vs. controls). We performed a two-way ANOVA to examine differences in the tolerance score. The model included continent (native vs. invasive) and insect type (specialist vs. generalist) as fixed factors.

We used mixed ANOVAS to examine differences in carbohydrate and protein contents and the ratio of carbohydrate to protein contents. The models included continent (native vs. invasive) as the fixed effect and plant populations nested within continent as the random effect. For the tannin contents, a similar approach was applied but the seedling age (year) was included as a fixed effect.

The populations planted and the spatial arrangement of plants varied among years for the chemical analysis study. To examine whether variation in populations across years could be driving the results for continent and year (i.e. differences in populations planted in each year could be causing an apparent continent \times year effect), we repeated the analyses with only the two populations present in all three of the first years and got qualitatively similar results. To examine whether the details of spatial arrangements of seedlings could be driving the results for continent and year (i.e. the planting of particular populations in particular locations in different years could be causing an apparent continent \times year effect), we tested whether spatial position (x, y coordinate for plot) was a significant predictor of tannins. It was not, and so we only present analyses that do not include predictors for spatial position.

When a significant effect was detected for an interaction term, further tests for differences among treatments were made using follow-up analyses that included only a subset of the data. For instance, to examine the effect of continent within a herbivore type, we performed a pair of follow-up analyses with only data from generalist or only from specialist treatments. We performed all data analyses with the statistical analysis software SAS, ver. 9.1 (SAS Institute Inc., Cary, NC, USA).

Results

LABORATORY EXPERIMENTS: PERFORMANCE OF SPECIALISTS AND GENERALISTS ON INVASIVE AND NATIVE POPULATIONS

Biomass of specialist larvae reared on leaves from invasive US populations was significantly greater than that of larvae reared

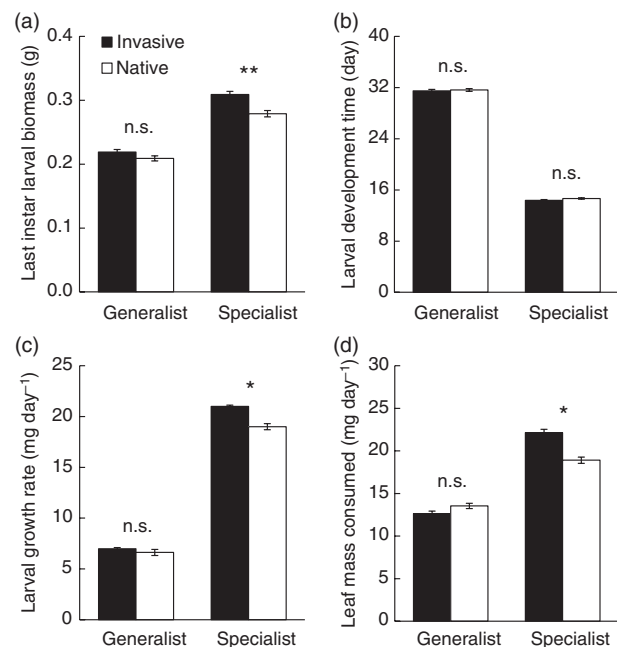


Fig. 1. Larval development indices of generalist and specialist caterpillars on the excised leaves from native and invasive populations in laboratory tests. Last instar larval biomass (a); larval development time from the first instar to pre-pupa (b); larval growth rate (larval biomass/developmental time) (c); and leaf mass consumed daily (d). Values are means \pm SE. P -value: * \leq 0.05; ** \leq 0.01; n.s., not significant.

on leaves from native Chinese populations (Fig. 1a). However, specialist development time was not affected by continental origin of tallow tree populations (Fig. 1b). The growth rate of specialist herbivores was significantly higher when larvae fed on the leaves of *Triadica* from invasive populations (US) compared to those from native populations (Fig. 1c). Specialists consumed more leaf biomass when fed foliage from invasive populations than when fed foliage from native populations (Fig. 1d). In contrast to the pattern for specialists, the generalist performed similarly on leaves from plants from the two continents (Fig. 1a–d).

COMMON-GARDEN EXPERIMENT: HERBIVORE PERFORMANCE AND PLANT REGROWTH AFTER HERBIVORY

Herbivore performance

Biomass of the specialist larvae fed on leaves from the invasive populations was significantly greater (30.8%) than that of larvae fed on leaves from native populations (Fig. 2a). Similarly, specialists consumed significantly more (43.3%) leaf area on invasive populations than natives (Fig. 2b). However, plant continent (native and invasive) did not affect larval biomass (Fig. 2a) and feeding areas (Fig. 2b) of the generalist. The specialist larvae consumed more leaf area than the generalist larvae (Fig. 2b), regardless of plant origin ($F_{1,110} = 342.84$, $P < 0.0001$).

Plant performance

Invasive plants grew rapidly (greater biomass and greater height) than native plants in nearly all treatment combinations (Fig. 3). Plant continental origin and its interaction with the generalist treatment significantly affected plant stem height and total biomass, but the corresponding effects of interaction between plant origin and the specialist treatment were not significant (Table 2). When herbivory was imposed, invasive plants performed better than natives regardless of the insect species (Table 2, Fig. 3). Both the generalist and specialist

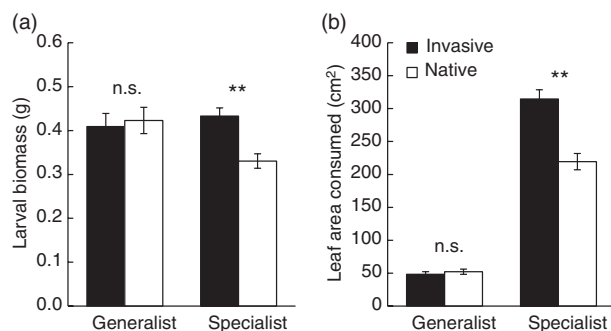


Fig. 2. Larval biomass (a) and feeding areas (per plant) (b) of the generalist and the specialist caterpillars on the leaves from native and invasive populations in common-garden experiments. One caterpillar was inoculated on each plant. Data were obtained 10 days after insect transfer. Values are means \pm SE. P -value: ** ≤ 0.01 ; n.s., not significant.

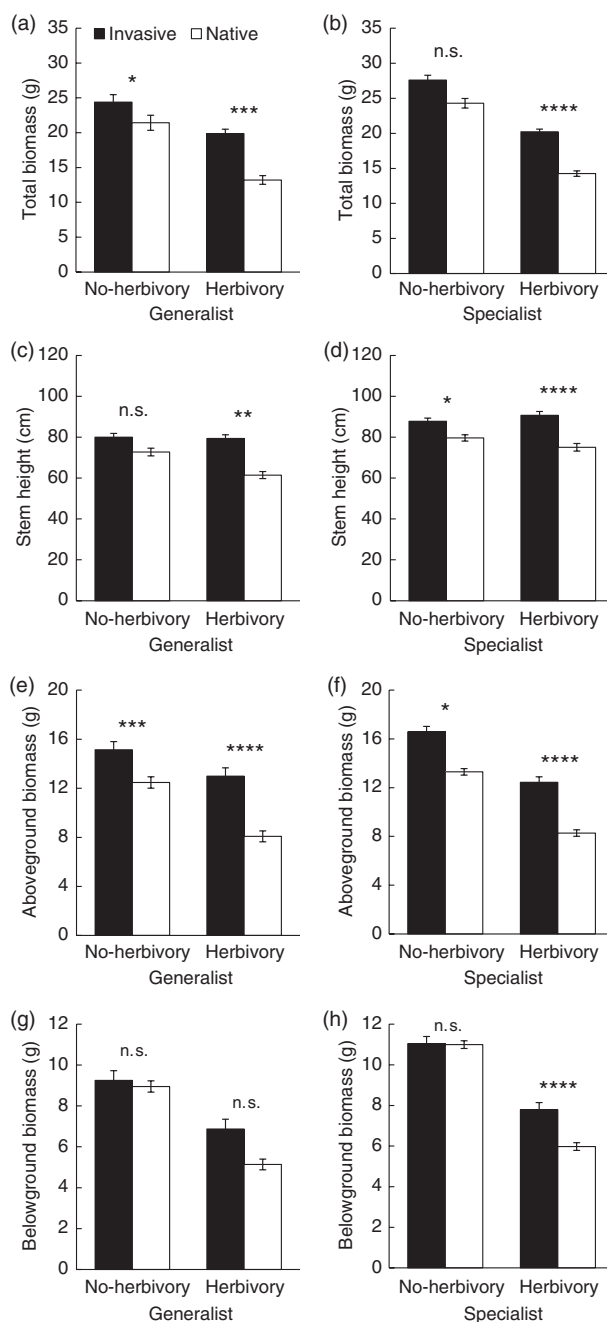


Fig. 3. Total biomass, stem height, above-ground biomass and below-ground biomass at the end of growing season with a generalist (a, c, e, g) and a specialist (b, d, f, h) caterpillar herbivore on the seedlings from native and invasive populations. When 100% defoliation was achieved, insects were removed from the cages. Plants then grew 100 days before harvest. Values are means \pm SE. P -value: * ≤ 0.05 ; ** ≤ 0.01 ; *** ≤ 0.001 ; **** ≤ 0.0001 ; n.s., not significant.

herbivory treatments suppressed plant growth (i.e. reduced total biomass) (Table 2, Fig. 3a,b).

For both of the generalist and specialist treatments, the patterns for total biomass were similar to those for above-ground biomass and stem height (Table 2). However, the patterns of the below-ground biomass differed from those for total and above-ground biomass. For example, below-ground biomass did not differ between the US and China populations, while

Table 2. A mixed nested analyses of variance for plant performance at the end of growing season. Continent: origin of the *Triadica* (native vs. invasive); treatment: herbivory or no herbivory. Conservative tests of origin differences were conducted using the corresponding population term as the associated error term

Response variable	Source of variation	Generalist			Specialist		
		d.f.	F-value	P-value	d.f.	F-value	P-value
Stem height	Continent	1,10	8.09	0.017	1,10	49.21	< 0.0001
	Treatment	1,91	10.55	0.002	1,94	0.24	0.626
	Population (Cont)	10,91	5.86	< 0.0001	10,94	0.99	0.459
	Treat × Cont	1,10	9.50	0.015	1,10	2.36	0.156
	Treat × Pop (Cont)	10,91	0.90	0.541	10,94	2.04	0.037
	Error	91			94		
Total biomass	Continent	1,10	22.80	0.001	1,10	12.39	0.006
	Treatment	1,91	50.77	< 0.0001	1,94	253.70	< 0.0001
	Population (Cont)	10,91	1.27	0.260	10,94	5.80	< 0.0001
	Treat × Cont	1,10	9.13	0.013	1,10	1.51	0.247
	Treat × Pop (Cont)	10,91	0.46	0.911	10,94	3.89	< 0.001
	Error	91			94		
Above-ground biomass	Continent	1,10	46.28	< 0.0001	1,10	12.18	0.006
	Treatment	1,91	32.16	< 0.0001	1,94	156.94	< 0.0001
	Population (Cont)	10,91	0.93	0.509	10,94	8.48	< 0.0001
	Treat × Cont	1,10	9.50	0.012	1,10	0.28	0.607
	Treat × Pop (Cont)	10,91	0.40	0.946	10,94	5.21	< 0.0001
	Error	91			94		
Below-ground biomass	Continent	1,10	1.46	0.254	1,10	3.22	0.103
	Treatment	1,91	62.20	< 0.0001	1,94	212.94	< 0.0001
	Population (Cont)	10,91	4.59	< 0.0001	10,94	3.31	0.001
	Treat × Cont	1,10	4.65	0.057	1,10	5.84	0.036
	Treat × Pop (Cont)	10,91	0.72	0.708	10,94	1.66	0.103
	Error	91			94		

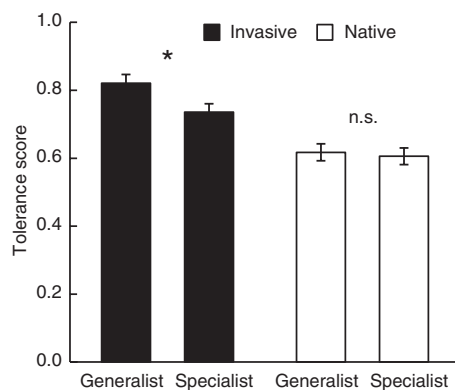


Fig. 4. Tolerance scores of the invasive and native *Triadica* populations as responses to herbivory by the generalist and specialist herbivores. Tolerance scores were calculated as the ratio of the total biomass for damaged plants divided by the mean value of undamaged control in the same herbivore treatment and population in the common-garden experiment. Values are means ± SE. *P*-value: * ≤ 0.05 ; n.s., not significant.

both total and above-ground biomass were higher for US populations.

Invasive plants showed greater tolerance to herbivory than natives, regardless of insect species (Fig. 4; $F_{1,10} = 21.55$, $P = 0.0009$). Native plants showed no difference in tolerance between generalist and specialist ($P = 0.739$); however, toler-

ance of invasive plants to herbivory by generalist was greater than by specialist (Fig. 4, $P = 0.012$).

NUTRIENT AND TANNIN CONTENTS

Native and invasive populations did not differ in carbohydrate and protein contents (Table 3, Fig. 5). However, invasive populations had a significantly higher ratio of carbohydrate to protein than native populations (Table 3, Fig. 5).

Invasive plants had lower tannin contents than native plants in all three different seedling age groups (Table 4, Fig. 6). Older seedlings appeared to produce more tannins than younger seedlings, regardless of their origin (Table 4, Fig. 6).

Discussion

The results of the laboratory and field garden experiments in this study clearly indicate that the invasive *Triadica* populations had lower resistance (Figs 1 and 2) and higher tolerance (Table 2, Figs 3 and 4) to the specialist caterpillar, *G. inexacta*, compared to native populations. Invasive populations were also more tolerant of the generalist caterpillar, *C. flavescentis*, than native populations (Fig. 4); however, introduced and native populations displayed similar resistance to the generalist caterpillar as larval development was comparable (Figs 1 and 2). Invasive populations showed faster growth compared to native counterparts when no herbivores were present (Fig. 3).

Table 3. A mixed nested analysis of variance for carbohydrate, protein and the ratio of carbohydrate to protein. Continent: origin of the *Triadica* (native vs. invasive). Conservative tests of origin differences were conducted using the corresponding population term as the associated error term

Source of variation	d.f.	Carbohydrate		Protein		Carbohydrate/protein	
		F-value	P-value	F-value	P-value	F-value	P-value
Continent	1,11	4.50	0.057	1.86	0.200	7.21	0.021
Population (Cont)	11,117	1.93	0.043	3.80	< 0.0001	1.90	0.046
Error	117						

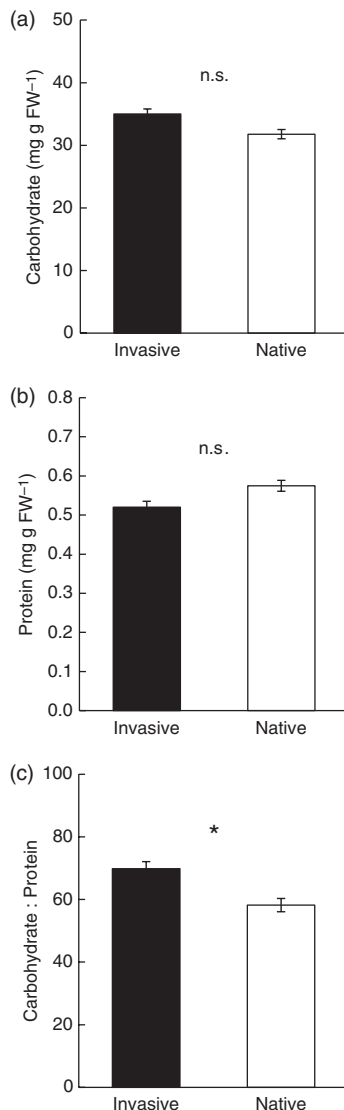


Fig. 5. Leaf carbohydrate (a) and protein (b) contents (fresh wt) and the ratio of carbohydrate to protein (c) in invasive and native populations. Values are means \pm SE. *P*-value: * \leq 0.05; n.s., not significant.

In the context of plant–insect interactions, herbivore resistance is a broad term for plant traits that reduce the preference or performance of herbivores, for example physical (e.g. surface waxes, trichomes and spines) or chemical defences (e.g. toxins, digestibility-reducers, and other secondary metabolites)

Table 4. A mixed nested analyses of variance for tannin content in seedlings at different ages. Continent: origin of the *Triadica* (native vs. invasive). Conservative tests of origin differences were conducted using the corresponding population term as the associated error term

Source of variation	d.f.	F-value	P-value
Continent	1,13	22.83	< 0.001
Year	3,252	125.89	< 0.001
Cont \times Year	2,8	0.75	0.503
Population (Cont)	13,252	1.81	0.042
Year \times Pop (Cont)	8,252	3.01	0.003
Error	252		

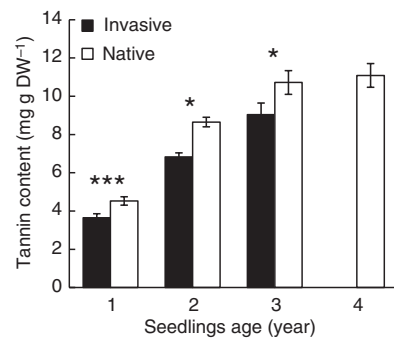


Fig. 6. Leaf tannin concentrations (dry wt) in seedlings of native and invasive populations at four different ages (years). Values are means \pm SE. *P*-value: * \leq 0.05; *** \leq 0.001; n.s., not significant.

(Beck 1965; Gatehouse 2002). In fact, the effectiveness of defences against different herbivore feeding guilds (e.g. root feeders, leaf chewers, phloem feeders, xylem feeders, galls) suggests that a broader consideration of herbivore feeding modes and plant strategies might be a productive extension of the EICA hypothesis. When EICA has been tested using foliage chewers, many previous studies have found more herbivore damage on invasive populations than natives when they were grown together in the field, indirectly indicating that resistance of invasive populations was lower than native populations (Wolfe, Elzinga & Biere 2004; Bossdorf *et al.* 2005; Zou *et al.* 2008; but see Cripps *et al.* 2009). However, field measurements potentially reflect not only defences that influence herbivore performance but also differences in herbivore feeding behaviour. In this study, increases in body size of larva reared from invasive populations vs. native populations provides

direct evidence for decreased resistance due to underlying differences in defence (Figs 1 and 2).

Our experiments reveal an altered chemistry in the invasive *Triadica* populations that may underlie their differences in herbivore resistance. Although the concentrations of carbohydrate and protein were similar between invasive and native populations, their ratios differed. This matches well with an earlier study that found higher C : N ratios in invasive populations (Siemann & Rogers 2001) since carbohydrates contain much of the carbon in a plant and proteins contain much of the nitrogen in a plant. Together these results indicate that *Triadica* constructs tissues relatively lower in proteins in its introduced range. In addition, in that same study a similar result was found for tannins: lower tannin contents in the invasive populations than in the native populations (Siemann & Rogers 2001). It is important to note that the results obtained here are from 1- to 4-year-old seedlings in the native range and the others are from 14-year-old *Triadica* trees in the introduced range. Thus, this suggests that the results found here are robust to details of venue and life stage.

The secondary chemical compounds of *Triadica* may play a key role in the resistance to herbivory. Tannins are known to be quantitative defensive components of plant quality (Müller-Schärer, Schaffner & Steinger 2004), having negative effects on the development and reproduction of herbivorous insects (Bernays 1981). Specialists and generalists may vary in their responses to tannins based on their level of adaptation to polyphenolics. For instance, Forkner, Marquis & Lill (2004) reported that specialists were more likely than generalists to correlate negatively with condensed tannins in *Quercus velutina* and *Quercus alba*. Lower tannin concentration in the foliage of invasive populations of *Triadica* could explain the rapid development and larger body size attained by *G. inexacta* compared to larvae feeding on native foliage. Contrary to the specialist moth, such differences in foliage quality appear not to affect the generalist *C. flavesceus* since it performed similarly on native and invasive populations (Figs 1 and 2). Thus, decreased resistance to specialists does not necessarily translate to increased resistance to generalists in *Triadica*, although generalists in other ranges have been found to cause higher damage to plants from invasive populations in common gardens (Siemann & Rogers 2003a) or to prefer them in choice feeding trials (Siemann & Rogers 2003b). Nevertheless, we only used tannins as a measurement of quantitative resistance; other foliar secondary compounds from *Triadica* deserve to be examined to fully understand the novel mechanisms involved in the invasive plant–herbivore interactions.

Tannins can be induced by damage (Nykänen & Koricheva 2004), thus results of feeding trials may be affected by experimental designs and source of plant materials. Tests in this study were performed with detached leaves in the laboratory and with intact leaves in the field common garden; however, their results were consistent. We do not exclude the possibility that the invasive and native plants are differentially inducible; their impact on insect performance, however, appears to be small when using detached leaves.

The results of the field common-garden study reveal an increased tolerance to herbivory by both the specialist and generalist moths in invasive populations (Fig. 4). As both the generalist and specialist moths are defoliating leaf chewers, the mechanism by which *Triadica* responds to herbivory (tolerance response) is most likely similar between the two. Given that many specialists in the native range and generalists in the introduced range are defoliators (Zheng *et al.* 2005), the invasive and native *Triadica* populations may share similar compensatory mechanisms in response to their corresponding natural enemies. Thus, although the specialists are absent, generalists in the introduced range could select for the maintenance of increased tolerance to herbivory in invasive populations (Müller-Schärer, Schaffner & Steinger 2004). However, generalist herbivores in *Triadica*'s introduced range cause little damage (Lankau, Rogers & Siemann 2004) which perhaps makes it more likely that greater herbivore tolerance of invasive populations is the result of selection for rapid growth rate (i.e. there is not likely strong selection for herbivore tolerance *per se* when damage is low).

Increased tolerance to herbivory by generalists might be related to decreased resistance in invasive *Triadica*. Zou *et al.* (2008) reported that the specialist beetle *Bikasha collaris* preferentially consumed leaf tissue of invasive populations of *Triadica* compared to native populations when given a choice, whereas the invasive populations tolerated herbivory more effectively than native populations. The proposed trade-off between resistance and tolerance to herbivory has also been reported in other plant species (Fineblum & Rausher 1995; Stastny, Schaffner & Elle 2005; Leimu & Koricheva 2006). The results of the current study are consistent with these patterns: we found that the specialist moth performed better on plants from invasive populations than on those from native populations and that plants from invasive populations tolerated feeding better than those from native populations in both the laboratory and field common-garden experiments (Figs 1–4). Whether this is the result of direct selection for increased tolerance, decreased resistance, or correlated traits such as growth rates, such variation in selection between invasive and native populations may promote adaptive divergence in plant defence.

Plant defence involves fitness costs (Strauss & Agrawal 1999; Strauss *et al.* 2002) and the costs of tolerance and resistance may differ between populations (Pilson 2000; Fornoni *et al.* 2004). The *Triadica* invasion may involve trade-offs between defence and growth, and between resistance and tolerance to generalists and specialists. The native populations showed stronger resistance to the specialist but slower growth than invasive populations, suggesting a trade-off between defence and growth, which supports the EICA hypothesis (Blossey & Nötzold 1995). The expression of costs of resistance is considered environment-dependent, thus the allocation costs of qualitative resistance (toxins such as alkaloids and glucosinolates) may be small, but high costs may be incurred by quantitative resistance (e.g. lignins and tannins) (see review in Strauss *et al.* 2002). In our study, because specialist insect performance was negatively affected when fed the natives in both the labora-

tory and field garden experiments but no such effects were found on the generalist, the cost of chemical resistance to the generalist may be less than the cost of resistance to the specialist. Given only generalists are present in the introduced range, the invasive plant populations may take this advantage to shift resources from resistance to tolerance, as we discussed earlier. If the cost of the defence (mainly tolerance) in the invasive populations is less than the cost of the defence (mainly resistance) in the native populations, the invasive populations likely obtain a net gain of resource in its introduced range, in response to the differing herbivore community. This resource may be invested into the plant growth in the introduced range, enabling faster plant growth.

Recent studies show the growth tolerance in a plant's early stage may result in a cost in reproduction in its late life stage (Brody, Price & Waser 2007). In this study, however, we focused on the tolerance of young *Triadica* seedlings, because previous studies indicate that the early seedling stage of *Triadica* is important in its invasion success (Bruce *et al.* 1997). Although we have no data that allow us to estimate fitness across many years, traits that are related to tolerance, such as the vigorous growth of young seedlings, indicate *Triadica* invasive populations may be very competitive with natives for resources (e.g. space, water, nutrients) that will benefit their growth and reproduction (e.g. Zou, Rogers & Siemann 2009).

The results of this study have important implications for biological control (Müller-Schärer, Schaffner & Steinger 2004). We predict that, if the specialist *G. inexacta* is introduced into the US for the control of *Triadica*, then the plant may support a superabundant population of the moth due to its low resistance. Our observation on the population dynamics of another specialist, a leaf-rolling weevil, *Heterapoderopsis bicallosicollis* on native and invasive *Triadica* supported this prediction (Y. Wang & J. Ding, unpubl. data). However, increased tolerance to defoliation will likely decrease the impact of the specialist on the plant. Overcoming this level of plant tolerance should be considered in such a biocontrol program.

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