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Decreased resistance and increased tolerance to native herbivores of the invasive plant *Sapium sebiferum*

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Release from natural enemies may favor invasive plants evolving traits associated with reduced herbivore-resistance and faster-growth in introduced ranges. Given a genetic trade-off between resistance and tolerance, invasive plants could also become more tolerant to herbivory than conspecifics in the native range. We conducted a field common garden study in the native range of *Sapium sebiferum* using seeds from native Chinese populations and invasive North American populations to compare their growth and herbivory resistance. We also performed a cage-pot experiment to compare their resistance and tolerance to *Bikasha collaris* beetles that are specialist feeders on *S. sebiferum* trees in China. Results of the common garden study showed that *Sapium* seedlings of invasive populations relative to native populations were more frequently attacked by native herbivores. Growth and leaf damage were significantly higher for invasive populations than for native populations. Growth of invasive populations was not significantly affected by insecticide spray, but insecticide spray benefited that of native populations. In the bioassay trial, beetles preferentially consumed leaf tissue of invasive populations compared to native populations when beetles had a choice between them. Regression of percent leaf damage on biomass showed that invasive populations tolerated herbivory more effectively than native populations. Our results suggest that *S. sebiferum* from the introduced range had lower resistance but higher tolerance to specialist herbivores. Both defense strategies could have evolved as a response to the escape from natural enemies in the introduced range.

Some invasive plants are more vigorous in their introduced range relative to their native range (Elton 1958, Crawley 1987, Blossey and Nötzold 1995, Mack et al. 2000, Bossdorf et al. 2005, Hawkes 2007). The invasive success of exotic plants may reflect evolutionary changes in introduced ranges (the post-introduction evolution hypothesis, Müller-Schärer and Steinger 2004). For example, the evolution of increased competitive ability (EICA) hypothesis proposes that invasive plants evolve reduced allocation to herbivore resistance and increased allocation to growth and/or reproduction because they are seldom attacked by natural enemies (e.g. herbivores and pathogens) in introduced ranges (Blossey and Nötzold 1995, Thompson 1998, Mooney and Cleland 2001, Bossdorf et al. 2005). Recent tests of the EICA hypothesis have produced inconsistent results (Daehler and Strong 1997, Willis et al. 2000, Vilà et al. 2003, Bossdorf et al. 2005, Franks et al. 2008).

While the EICA hypothesis postulates that the successful invasion of exotic plants reflects an evolutionary response to decreased defensive investments, herbivore defense may involve both resistance (reducing herbivore attack) and tolerance strategies (buffering the negative fitness impacts of herbivory, van der Meijden et al. 1988, Tiffin 2000, Juenger and Lennartsson 2000, Müller-Schärer et al. 2004). Tolerance to herbivory is the capacity of a plant to maintain its fitness through growth and reproduction after sustaining herbivore damage. A trade-off between resistance and tolerance is predicted by ecological theory, and intraspecific comparisons suggest that reduced resistance may translate into increased tolerance to herbivory (Rosenthal and Kotanen 1994, Fineblum and Rausher 1995, Strauss and Agrawal 1999, Tiffin and Rausher 1999, Stowe et al. 2000, Stastny et al. 2005). In addition, growth and tolerance traits may be genetically correlated because fast-growing plants are able to increase tolerance when there is time for compensatory growth after herbivore attack (Weis et al. 2000). Therefore, we might expect invasive species to be faster-growing and less herbivore-resistant but more herbivore-tolerant compared to conspecifics in the native range. When they are grown in the presence of specialist herbivores, plants from invasive populations would be more damaged by herbivores due to their decreased resistance, but increased tolerance would give them greater ability to compensate at similar levels of damage. However, few studies have simultaneously examined herbivory resistance and tolerance of invasive plants (Bossdorf et al. 2004, 2005, Stastny et al. 2005).

Consistent with the EICA hypothesis predictions, studies on Chinese tallow tree *Sapium sebiferum*, Euphorbiaceae, synonyms include *Triadica sebifera*, "*Sapium*" henceforth, in the introduced range (North America) suggest that *Sapium* has become a faster-growing and less herbivore-resistant plant in response to low herbivore loads in its introduced range (Siemann and Rogers 2001, 2003a, b, Siemann et al. 2006). In a 14-yr common garden study, for instance, plants of invasive Texas populations were larger, yet more poorly defended chemically against herbivores than native Asia populations (Siemann and Rogers 2001). Studies with simulated herbivory also suggest that invasive *Sapium* has evolved to be a more herbivore-tolerant plant (Rogers and Siemann 2004, 2005). Invasive populations of *Sapium* were found to have greater compensatory ability than native populations when they had undergone simulated root damage (Rogers and Siemann 2004) or simulated leaf damage (Rogers and Siemann 2005). Generalist grasshoppers in the introduced range preferred seedlings from invasive populations over those from native populations of *Sapium* in bioassay trials, but invasive populations had greater compensatory growth following herbivore damage (Rogers and Siemann 2005). These results indicate that invasive populations of *Sapium* tolerate herbivory more effectively relative to native populations.

In these studies, the relative performances of native and invasive populations of *Sapium* were compared in the introduced range (Siemann and Rogers 2001, 2003a, b, Siemann et al. 2006) or under simulated herbivory conditions (Rogers and Siemann 2004, 2005). Simulated damage may not be an adequate mimic of real insect herbivory in the native range (van Kleunen and Schmid 2003, Meyer et al. 2005). If simulated damage is a poor surrogate for herbivory, it may not give an accurate measurement of herbivore tolerance (Agrawal 1998, Strauss and Agrawal 1999, Tiffin and Inouye 2000). In addition, some studies indicate that resistances against specialists and generalists are likely based on different mechanisms (Müller-Schärer et al. 2004, Joshi and Vrieling 2005, Leger and Forister 2005, Müller and Martens 2005), suggesting that EICA studies addressing specialist herbivores may find different results with those addressing generalist herbivores (Bossdorf et al. 2005). If a species experiences different enemy regimes in its native and introduced ranges, the study outcome may differ between native and introduced ranges (van Kleunen and Schmid 2003, Wolfe et al. 2004, Meyer et al. 2005). To our knowledge, however, no studies on *Sapium* have been conducted in the presence of specialist herbivores or under natural herbivory conditions in the introduced range.

To test the hypothesis that invasive *Sapium* has become a faster-growing, less herbivore-resistant and more herbivore-tolerant plant compared to conspecifics from the native range, we performed a common garden field experiment in *Sapium*'s native Chinese range. In this experiment, *Sapium* seedlings of native and invasive populations were grown with or without insecticide spray. We predicted that 1) growth rate of *Sapium* seedlings would be greater for invasive populations than for native populations; 2) seedlings of invasive populations would be more frequently attacked by native herbivores given that invasive populations are less well defended than native populations; and 3) insecticide spray would more benefit growth of native populations than that of invasive populations because greater compensatory ability is expected to buffer the negative impacts of herbivory on invasive populations. In addition, we conducted a cage-pot experiment with a native specialist beetle species, *Bikasha collaris*, a Chrysomelid that is one of major pests on *Sapium sebiferum* trees in China (Zheng et al. 2004). We predicted that 1) beetles would prefer plants from invasive populations over those from native populations when beetles had a choice between them; and 2) herbivory would have a significant impact on seedling growth of native populations, while growth of invasive populations would be less affected by herbivory.

Material and methods

Study species

The introduced Chinese tallow tree is an invasive plant that aggressively displaces native plants and forms monospecific stands in the southeastern USA (Bruce et al. 1997). *Sapium* seedlings grow rapidly and its generation time is ca 3–4 yr in good growing conditions. *Sapium* is native to China, where it is naturally occurring and has been cultivated for 14 centuries (Zhang and Lin 1994, Bruce et al. 1997). In China, the natural distribution of *Sapium* ranges from 18°31′ to 34°40′N, and from 98°40′ to 122°E (Zhang and Lin 1994). *Sapium* was first introduced to Georgia in the late 18th century from Asia for wood and oil production by Benjamin Franklin (ca 1772) and later to Texas and Louisiana in the early 1900s as an ornamental or potential seed oil crop species (Bruce et al. 1997). The later introduction was conducted by the Bureau of Plant Industry (US Dept of Agriculture) before they began keeping systematic records of plant material sources (Cameron and Spencer 1989, Jubinsky 1994). Genetic analyses suggest that these two introductions are likely from different sources in China. Texas populations are more closely related to contemporary northern Chinese populations while Georgia populations are more closely related to contemporary southern Chinese populations (DeWalt et al. 2006, unpubl.).

Seeds collection

In November and December 2004, we hand collected seeds from nine provinces (states) in the native Chinese and introduced North American ranges of *Sapium* (Table 1). Seeds were collected from 4 to 10 different trees of each site and stored in the dark at low temperature until planting in December 2006. Seeds were planted in 65 ml cone-tainers (Stuewe and Sons, Corvallis, OR, USA) in a greenhouse at Nanjing Agricultural Univ., Nanjing, Jiangsu, China (32°2′N, 118°50′E). Cone-tainers were filled with soil taken from the top 20 cm of the profile in fields where some

Table 1. Native (Chinese) and invasive (USA) populations of *Sapium sebiferum* that were used in this study. Seeds from different locations in the states of Texas or Georgia were treated as a single TX or GA population, respectively. Seeds from Jiangsu (JSU) and Anhui (ANH) provinces were treated as northern Chinese populations (CHN) and those from Fujian (FUJ) and Guangdong (GUD) provinces as southern Chinese populations (CHS) in the cage-pot experiment.

Population	Location	Latitude	Longitude
Native			
JSU	Nanjing, Jiangsu province	32°2′N	118°50′E
ANH	Hefei, Anhui province	31°36′ ~32°2′N	117°11′ ~118°2′E
ZHE	Hangzhou, Zhejiang province	30°16′N	120°8′ ~11′E
HUN	Zhangjiajie, Hunan province	29°18′N	110°30′E
JXI	Taihe, Jiangxi province	25°55′ ~26°39′N	114°38′ ~55′E
FUJ	Xiamen, Fujian province	24°26′N	118°5′E
GUD	Guangzhou, Guangdong province	23°5′ ~46′N	113°17′ ~53′E
Invasive			
TX	La Marque, Texas	29°22′N	95°3′W
	Houston, Texas	29°41′ ~43′N	95°24′ ~25′W
	Port Arthur, Texas	29°53′N	94°2′W
GA	Sapelo Island, Georgia	31°24′N	81°16′W
	Savannah, Georgia	32°7′N	81°6′W
	Hutchinson Island, Georgia	32°10′N	81°9′W

Sapium trees are naturalized. Planted seeds remained dormant throughout the winter season and germinated during March. It is documented that rapid growth of *S. sebiferum* seedlings during the year of germination is comparable to or greater than that of adjacent native species in the introduced range, whether in deep shade or forest gaps, suggesting that the early seedling stage plays an important role in its invasion success (Bruce et al. 1997). Thus, this study used first-year *S. sebiferum* seedlings to test our predictions. To minimize maternal effects due to differences in seed quality, seedlings of uniform condition (similar height and leaf numbers and no insect damage) were selected for use in this study.

Field experiment design

In April 2007, a common garden was established in a 15 × 20 m grid of an abandoned field at the field station of Nanjing Agricultural Univ., Nanjing, China. There are natural *Sapium* trees in the vicinity and thus natural herbivores can easily access the field to feed on *Sapium* seedlings. Eighty *Sapium* seedlings of native populations (10 ANH, 12 FUJ, 10 FUN, 14 GUD, 10 JSU, 10 JXI, and 14 ZHE, Table 1) and 80 *Sapium* seedlings of invasive populations (30 GA: 8 Sapelo Island, 12 Savannah, 10 Hutchinson Island, and 50 TX: 16 La Marque, 24 Houston, 10 Port Arthur) were individually transplanted into 1 × 1 m plots with or without insecticide (Esfenvalerate) spray. During the growing season, insecticide was sprayed twice a month for insecticide treatments and water spray served as controls. We checked seedling survival and measured seedling height, damaged/killed seedlings, total number of leaves and damaged leaves per seedling monthly through May to September (five times). At the beginning of October, shoots of each seedling were harvested, dried at 60°C for 3 d and weighed separately. The average leaf area removal per damaged seedling was visually estimated by a 5% interval category. Total leaf area removal per damaged seedling was calculated by multiplying the average removal per damaged leaf by the proportion of damaged leaves per seedling.

Pot experiment set-up

Seeds used in the cage-pot experiment were the same source as those in the field common garden. Because we were more interested in evolutionary changes in herbivory resistance and tolerance between origins (continents) than variation among populations within the same continent in this short-term bioassay trial, seeds collected from the most northern areas of *Sapium* in China (Jiangsu–JSU and Anhui–ANH provinces) were treated as northern Chinese (CHN) populations and those from the most southern areas (Fujian–FUJ and Guangdong–GUD provinces, Table 1) as southern Chinese (CHS) populations (Zou et al. 2008). Plants from different provinces within the southern or northern areas likely experience similar climates (Zhang and Lin 1994), while northmost and southmost populations were separated by many hundreds of kilometers. A laboratory feeding trial showed no significant difference in *Sapium* seedling performance or herbivore damage between seedlings from Fujian and Guangdong provinces (Siemann and Rogers, 2003a). Seeds from Texas (TX) and Georgia (GA) were treated as different invasive populations.

At the beginning of May, seedlings of uniform condition from native (CH) and invasive (US) populations were individually transferred into 192 10-l tree-pots filled with field collected topsoil. Average height and number of leaves were 73.3 mm and 2.5 for US seedlings, and 72.9 mm and 2.8 for CH seedlings. These seedling pots were combined to form 6 types of pairs (TX–GA, TX–CHN, TX–CHS, GA–CHN, GA–CHS, and CHN–CHS, Fig. 1). Each pair was replicated 16 times. We installed nylon mesh cages for each pair of tree-pots. The height of each cage was 0.8 m and the mesh size was small enough to prevent beetle escape. The paired-pots were randomly arranged, watered as needed and re-randomized weekly during the course of the experiment. The pots were placed in a screenhouse at Nanjing Agricultural Univ., Jiangsu, China.

Many species of arthropods consume *Sapium* trees in China. Chrysomelid *Bikasha collaris* (synonym: *Aphthonomorpha collaris*) beetles are reported to be one of the primary specialist herbivores that feed on *Sapium sebiferum* in China (Zheng et al. 2004). It is one of the most

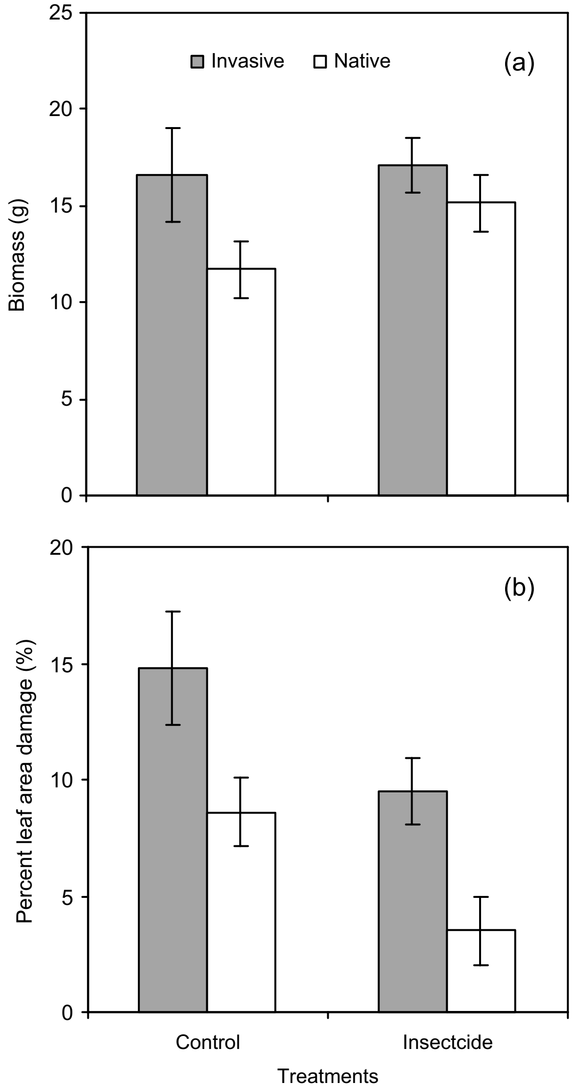

Figure 1. Mean (±1 SE) shoot biomass (a) and percent leaf area damage (b) of *Sapium* seedlings as affected by the continental origin and insecticide. Data were collected at the end of the field common garden experiment. Statistical significance is shown in Table 3.

abundant feeders that are responsible for the majority of leaf damage in Nanjing (unpubl.). We caught adult beetles on *Sapium* trees that were growing in the surrounding vicinity. These beetles were starved for at least 24 h before they were placed in the screen cage. We placed one beetle in each cage on days 2, 7, 13, 19, and 25, and thus 5 beetles were caged in each pot by the end of bioassay. Beetles could freely access both seedlings within each cage. All seedlings survived over the entire experiment. All combinations of seedling type and seedling pairs experienced some chewing by the beetles.

On day 30, we removed beetles from all cages and harvested half of the seedling pots (8 cages for each pair type, i.e. 96 seedlings) to compare leaf damage between two population types of *Sapium.* The rest of the seedlings were grown for an additional month after cessation of herbivory. On day 60, we harvested and measured shoots of each seedling to examine the herbivory impact on seedling growth. For the seedlings harvested on day 30, fresh leaves of each seedling were scanned on a flatbed scanner. We measured total leaf area including (Potential leaf area) and excluding damaged parts (Leaf area remaining) using the computer program ScionImage (Scion Image for Windows, Scion Corporation, <www.scioncorp.com>). This program is based on NIH Image, which has been used to calculate leaf area in previous studies (Siemann and Rogers 2003a). Percent leaf damage of each seedling was calculated as [(Potential leaf area–Leaf area remaining)/Potential leaf area × 100].

Statistical analyses

All statistical analyses were conducted using JMP, ver. 5.1 (SAS Inst., Cary, NC, USA). For the field experiment, data were analyzed using nested analysis of variance (ANOVA), where continent of origin and insecticide were considered as fixed factors, and population was nested within continent of origin. Effects of continent were tested over the nested population term. In the repeated-measure ANOVAs, the between subject effects refer to plants, and the within subject effects refer to the five census times (Table 2). Average seedling height growth rate was calculated as [(measured height–initial height)/initial height/days since planting × 1000]. The height growth, proportion of damaged leaves per seedling and proportion of damaged/killed seedlings were cube-root transformed, and the percent leaf removal of damaged seedlings was fourth-root transformed to achieve normality and homoscedasticity.

To examine the difference in leaf area remaining and percent leaf area damage between native and invasive population types in the cage-pot experiment, we used a paired t-test when paired seedlings in one cage were from different continents (CHN–GA, CHN–TX, CHS–GA, CHS–TX), and an unpaired t-test for cages in which paired seedlings were from the same continent (CHS–CHN cages vs TX–GA cages). We tested whether percentage of leaf area damage depended on the population within the same continent using an additional paired t-test (CHS–CHN or TX–GA). The Bonferroni-adjusted critical value was considered for nonindependent comparisons when we calculated t-test for the various seedling combinations. The true critical alphas for the tests are somewhere between unadjusted and the adjusted alphas (García 2004). Percent leaf damage was square-root transformed for statistical analyses.

Similar to fitness reaction norms of populations exposed to different damage levels (Strauss and Agrawal 1999, Stowe et al. 2000, Agrawal et al. 2004), herbivory tolerance was calculated as the slope of the regression of percent leaf damage on seedling biomass (Fig. 3). In the regression analyses, the intercept refers to biomass under undamaged conditions (potential growth) and the slope represents herbivory tolerance (the negative impacts of herbivory). A t-test was used to examine significance of the intercept and slope in the regressions. We conducted an ANCOVA on seedling biomass with continent as the main effect and percent leaf damage as the covariate. A significant interaction (difference in regression slope) was interpreted as difference in tolerance between the two continent types.

Table 2. Repeated-measures analysis of variance on the difference between native and invasive populations in *Sapium* seedling growth and herbivory damage. "Origin" indicates native (China) or invasive (USA) range. "Time" represents the time of seedling growth and herbivory damage measurements. Damaged leaves and seedlings refer to the proportion of the number of damaged leaves and damaged seedlings, respectively. Height growth, damaged leaves and damaged seedlings data were cube-root transformed.

Source	Height growth				Damaged leaves				Damaged seedlings			
	DF	SS	F	p	DF	SS	F	p	DF	SS	F	p
Between subjects												
Origin	1	0.24	3.94	0.05	1	0.52	4.25	0.04	1	0.42	4.31	0.04
Insecticide	1	0.04	0.64	0.43	1	1.20	9.88	0.002	1	0.58	5.85	0.02
Pop. [Orig.]	7	0.75	1.79	0.10	7	0.48	0.56	0.78	7	0.30	0.44	0.87
Origin × Insecticide	1	0.12	1.94	0.07	1	0.19	1.53	0.22	1	0.07	0.67	0.41
Pop. × Insecticide [Orig.]	7	0.05	0.75	0.39	7	0.70	0.82	0.57	7	0.07	1.01	0.43
Plants	153	9.20			126	15.30			126	12.40		
Within subjects												
Time	4	60.81	101.36	<0.0001	4	0.24	0.14	0.97	4	0.05	0.08	0.99
Time × Origin	4	0.37	0.62	0.65	4	0.28	0.16	0.96	4	0.12	0.18	0.94
Time × Insecticide	4	0.31	0.52	0.72	4	0.85	0.48	0.75	4	0.28	0.42	0.79
Time × Pop. [Orig.]	28	2.43	0.58	0.90	28	6.43	0.52	0.94	28	2.43	0.53	0.93
Time × Insecticide × Origin	4	0.05	0.08	0.99	4	0.33	0.19	0.94	4	0.15	0.23	0.92
Time × Insecticide × Pop. [Orig.]	28	1.20	0.29	1.00	28	4.95	0.40	0.98	28	1.87	0.41	0.98
Error	153	22.95			126	55.5			126	20.70		

There were no significant differences in the slope or intercept between populations within each continent, therefore we did not discriminate in regression analyses between TX and GA or CHS and CHN populations (Fig. 3).

Results

Field experiment

Height growth rate decreased with time but no significant interaction of time with treatments was found. Over the entire growing season, height growth rate was significantly higher for invasive populations than for native populations (Table 2). Harvested seedling shoot mass of invasive populations was significantly greater than that of native populations (Table 3, Fig. 1a). A pronounced interaction between origin and insecticide on height growth and biomass suggested that insecticide spray benefited native population growth, while growth of invasive populations was not significantly affected by herbivory (Table 2 and 3, Fig. 1a).

Insecticide spray significantly reduced damaged leaves, damaged/killed seedlings and leaf damage level for both native and invasive populations (Table 2 and 3, Fig. 1b). Damaged/killed seedlings and proportion of damaged leaves per seedling were significantly greater for invasive populations relative to native populations, which was independent of measuring time (Table 2). For damaged seedlings, percent leaf area damage by herbivory was significantly higher for invasive populations than for native populations (Table 3, Fig. 1b). Seedling growth, leaf damage and damaged/killed seedlings did not significantly differ among populations within each continent or its interaction with insecticide (Table 2 and 3).

Cage experiment

In general, invasive populations had significantly greater leaf area remaining than native populations whether paired seedlings in one cage were from different continents (Fig. 2a, term "US–CH") or the same continent (CHS–CHN versus GA–TX, unpaired t-test, $p = 0.03$). Specifically, greater leaf area of invasive populations relative to native populations was found for seedling pairs of TX–CH, TX–CHN, GA–CH, and GA–CHS, but no significant difference in leaf area was found for the pair of TX–CHS or GA–CHN (Fig. 2a). When beetles had a choice between two population types in one cage (i.e. paired seedlings in one cage were from different continents), percent leaf damage was significantly higher for invasive populations compared to native populations (Fig. 2b). Percent leaf area damage did not significantly differ between populations within the same continent (Fig. 2b, term "TX–GA", "CHS–CHN"). When beetles did not choose between seedlings of native and invasive populations (i.e. paired seedlings in one cage were from the same continent), percent leaf damage did not significantly differ between two population types (TX–GA cages versus CHN–CHS cages, unpaired t-test, $p = 0.10$).

Table 3. ANOVAs on the difference between native and invasive populations in *Sapium* seedling growth and percent herbivory damage at the end of field experiment. Terms are the same as in Table 2.

Source	Shoot biomass				Percent leaf area damage			
	DF	SS	F	p	DF	SS	F	p
Origin	1	331.9	42.4	<0.0001	1	7.9	8.9	0.003
Insecticide	1	247.1	31.3	<0.0001	1	5.9	6.6	0.01
Pop. [Orig.]	7	36.8	0.7	0.70	7	5.1	0.8	0.57
Origin × Insecticide	1	36.8	4.6	0.03	1	0.3	0.3	0.57
Pop. × Insecticide [Orig.]	7	62.3	1.1	0.35	7	9.0	1.5	0.19
Model	17	835.5	6.2	<0.0001	17	25.8	1.7	0.05
Error	153	1208.0			126	126.0		

Herbivory had a significant cost to native populations as depicted by significant impacts of percent leaf damage on shoot biomass, while its cost to invasive populations was not pronounced (Fig. 3, Native genotype: slope = −0.239, $p < 0.001$, Invasive genotype: slope = −0.0681, $p = 0.08$). A difference in the slopes of regression line suggested that invasive populations of *Sapium* tolerated herbivory more effectively than native populations (Interaction term: $p = 0.008$). In the regressions, larger shoot biomass (greater intercept) is expected to be associated with invasive populations under undamaged conditions, suggesting invasive populations potentially grew faster than native populations (Native genotype: intercept = 5.18, $p < 0.001$; Invasive genotype: intercept = 6.13, $p < 0.001$).

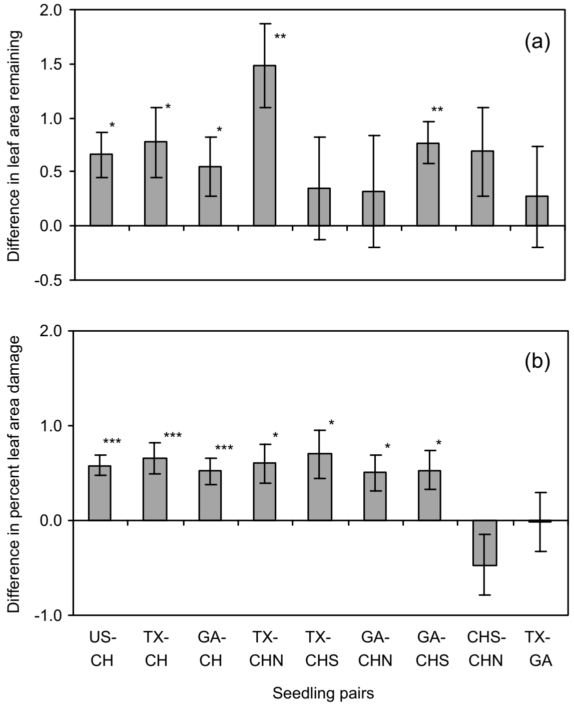

Figure 2. Mean differences in leaf area remaining (a) and percent leaf area damaged by beetles (b) between native and invasive populations in cage-pot experiment. See text for definition of terms. The term "US–CH" signifies overall difference in performance between invasive North American populations and native Chinese populations. Positive performance differences denote that leaf area remaining or percent leaf area damage was greater in the first member of the pair (e.g. the positive difference between US–CH shows that US populations had greater leaf area remaining or leaf damage than CH populations). Error bars represent ±1 standard error. Statistical significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Discussion

The EICA hypothesis predicts that invasive plants evolve an increase in growth and a reduction in resistance to herbivory in response to low herbivory loads in their introduced range (Blossey and Nötzold 1995, Bossdorf et al. 2005). In the common garden field study, height growth and harvested shoot mass were significant greater for invasive populations than for native populations. Damaged/killed seedlings, proportion of damaged leaves per seedling and percent leaf damage of invasive populations relative to native populations were significantly greater, suggesting that

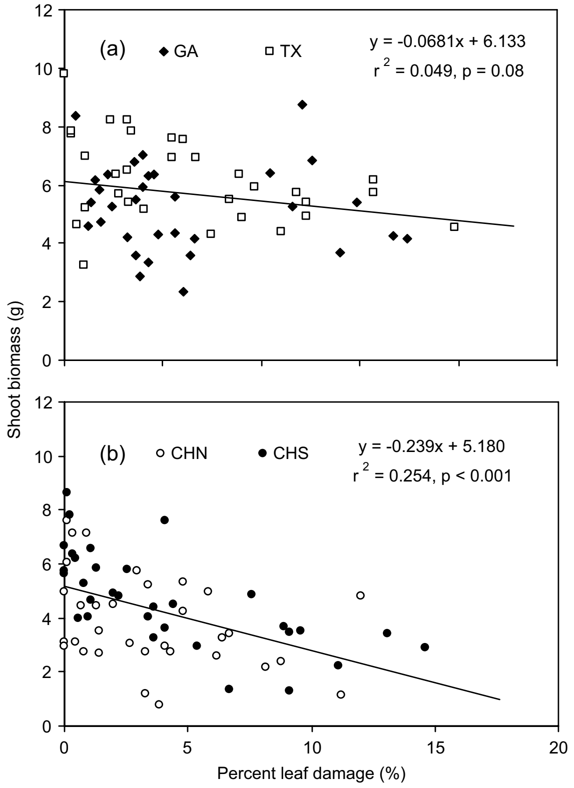

Figure 3. Regression of percent leaf damage on shoot biomass for seedlings of invasive North American (a) and native Chinese (b) populations of *Sapium sebiferum* when paired seedlings in one cage were from different continents in bioassay trial.

seedlings of invasive populations were more frequently attacked by native herbivores in the native Chinese range. In the bioassay trial, we found that beetles consumed more leaf area of invasive populations than native populations when they had a choice between the two population types. Together these results suggest that plants of invasive populations were less resistant to native herbivores than those of native populations, which is consistent with the EICA hypothesis prediction.

Invasive species may have different mechanisms to defend against generalist and specialist herbivores (Müller-Schärer et al. 2004, Joshi and Vrieling 2005, Leger and Forister 2005, Müller and Martens 2005). The results of the cage-pot study with native specialist beetles are consistent with previous studies in the introduced North American range where *Sapium* seedlings were primarily consumed by generalists (Siemann and Rogers 2001, 2003a, Siemann et al. 2006). Generalist beetles from Asia preferred plants from introduced populations over those from native populations in common gardens in Hawaii (Siemann and Rogers 2003b). Together these results indicate that invasive *Sapium* has reduced resistance to both generalist and specialist herbivores compared to conspecifics in the native range. This is in contrast with increased resistance to generalists but reduced resistance to specialists found for *Eschscholzia californica* (Leger and Forister 2005), *Lepidium draba* (Müller and Martens 2005), and *Senecio jacobaea* (Joshi and Vrieling 2005).

If there is a genetic correlation between plant vigor and tolerance traits of invasive plants, reduced resistance may translate into increased tolerance to herbivory (Rosenthal and Kotanen 1994, Fineblum and Rausher 1995, Strauss and Agrawal 1999, Tiffin and Rausher 1999, Stowe et al. 2000, Stastny et al. 2005). This hypothesis is supported by the result of this feeding trial showing that faster-growing plants from invasive populations had lower resistance, but tended to tolerate herbivory better than those from native populations (Fig. 2b and 3), and by the result of field common garden study showing that insecticide spray more benefited growth of native populations than that of invasive populations (Table 3, Fig. 1a). In a four-month pot experiment in the native range in the presence of herbivores, plants from invasive populations tolerated herbivory more effectively than those from native populations of *Sapium* (Zou et al. 2008). Greater compensatory ability of invasive populations relative to native populations was also found when they had undergone simulated root damage (Rogers and Siemann 2004) or simulated leaf damage (Rogers and Siemann 2005). These results suggest that invasive *Sapium* could have evolved to be fast-growing and herbivore-tolerant plants in the introduced range.

Tolerance has received relatively little attention in the context of plant invasion (Bossdorf et al. 2004, 2005, Stastny et al. 2005). In particular, few studies have simultaneously examined resistance and tolerance of invasive plants under natural herbivory conditions (Bossdorf et al. 2005, Stastny et al. 2005). Increased tolerance could contribute to invasive populations outperforming native populations despite being more frequently attacked by herbivores due to reduced resistance when they are grown in the native range if differences in degree of damage are small or absolute damage levels are low. Greater growth and herbivory damage of invasive populations relative to native populations were found in *Sapium sebiferum* by a previous study in the native range (Zou et al. 2008), in *Silene latifolia* (Wolfe et al. 2004) and in *Senecio jacobaea* (Stastny et al. 2005). In contrast, herbivore tolerance was speculated to be lower in invasive populations relative to native populations of *Solidago gigantea* (Meyer et al. 2005). Similar levels of tolerance between native and invasive populations were found in *Alliaria petiolata* (Bossdorf et al. 2004) and in *Solidago canadensis* (van Kleunen and Schmid 2003).

If both resistance and tolerance strategies vary among populations of invasive plants, whether or not percent leaf damage of plants differs between native and invasive populations in common gardens may depend on their compensatory capacity relative to herbivory levels. Given a higher compensatory ability of invasive populations following herbivore attack, no significant difference in realized leaf damage would be expected between two populations when they experience small amounts of herbivory. In previous common garden studies in *Sapium*'s introduced North American range where leaf damage was typically $<5\%$ (0.24% Siemann and Rogers 2001, 0.14–0.35% Siemann and Rogers 2003a, 2–4% Siemann et al. 2006), no significant difference in percent leaf damage was found between two population types, although chemical resistance level (e.g. tannins) was found to be lower for invasive populations than for native populations. When herbivory was so high that invasive populations could not completely compensate for damage losses in a common garden in Hawaii, however, percent leaf damage was higher for invasive populations than for native populations (Siemann and Rogers 2003b). Percent leaf damage was also found to be significantly greater or tended to be higher for invasive populations relative to native populations in previous pot experiments in the native range of *Sapium* where herbivory was high (typically 10–20%, Zou et al. 2006, 2008).

Larger leaf area remaining of invasive populations relative to native populations in the feeding choice trial suggests that increasing leaf area could be used as a tolerance strategy by invasive plants. Higher tolerance plants may expand total leaf area by compensatory growth following herbivory (Tiffin 2000). Given a similar plant photosynthetic efficiency, greater leaf area will allow invasive plants to use light more efficiently. This tolerance strategy of invasive plants could have evolved in the introduced range via selection on rapid growth in general. In previous common garden studies, we found that plants from invasive populations relative to native populations of *Sapium* exhibited greater total leaf area, lower ratio of root to shoot and higher photosynthetic rate by which invasive populations attained higher relative growth rates (Zou et al. 2006, 2007). In addition, invasive populations of *Sapium* can use soil nutrients more efficiently than those from native populations (Zou et al. 2006). The interplay of these genetic shifts in traits may give rise to *Sapium*'s capacity to regrow after herbivore damage, and thus increase tolerance to herbivory. Indeed, invasive plants often have greater relative growth rate, higher net CO_2 assimilation, and more biomass allocated from root to shoot and photosynthetic tissues when compared with other species (Grotkopp et al. 2002) or with their conspecifics from the native ranges (Bastlová and Květ 2002, Erfmeier and Bruelheide 2005, Buschmann et al. 2005, Güsewell et al. 2006). These traits may have increased the compensatory ability of invasive plants following herbivory.

A trade-off between resistance and tolerance has important implications for biological control of invasive plants (Rogers and Siemann 2004, Müller-Schärer et al. 2004, Stastny et al. 2005). If effective tolerance mechanisms are common in invasive plants, introductions of insect biological control agents would be expected to exhibit only weak negative effects on their hosts. On the other hand, the population of biological control agents would be abundant over extended time periods because they are not regulated by plant tolerance at all, or as strongly as resistance (Müller-Schärer et al. 2004). Unfortunately, comparisons of herbivore tolerance between native and invasive populations have been largely neglected, and few studies have examined genetic shifts in intrinsic traits that are considered fundamental mechanisms for herbivory tolerance of invasive plants. Certainly, these studies deserve to be conducted in the future.

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