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Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*

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Abstract The evolution of increased competitive ability (EICA) hypothesis predicts that release from natural enemies in the introduced range favors exotic plants evolving to have greater competitive ability and lower herbivore resistance than conspecifics from the native range. We tested the EICA hypothesis in a common garden experiment with *Sapium sebiferum* in which seedlings from native (China) and invasive (USA) populations were grown in all pairwise combinations in the native range (China) in the presence of herbivores. When paired seedlings were from the same continent, shoot mass and leaf damage per seedling were significantly greater for plants from invasive populations than those from native populations. Despite more damage from herbivores, plants from invasive populations still outperformed those from native populations when they were grown together. Increased competitive ability and higher herbivory damage of invasive populations relative to native populations of *S. sebiferum* support the EICA hypothesis. Regression of biomass against percent leaf damage showed that plants from invasive populations tolerated herbivory more effectively than those from native populations. The results of this study suggest that *S. sebiferum* has become a faster-growing, less herbivore-resistant, and more herbivore-tolerant plant in the introduced range. This implies that increased competitive ability of exotic plants may be associated with evolutionary changes in both resistance and tolerance to herbivory in the introduced range. Understanding these evolutionary changes has important implications for biological control strategies targeted at problematic invaders.

Keywords Biological invasions · Biological control · EICA hypothesis · Enemy release · Herbivore resistance · Herbivore tolerance

Introduction

Biological invasion has been recognized as a major threat to biodiversity second only to habitat destruction (Vitousek et al. 1996; Wilcove et al. 1998). One explanation for the increased abundance and vigor of many invasive plants in their introduced range relative to their native range concentrates on the lack of co-evolved natural enemies (e.g., herbivores and pathogens). Exotic plants released from natural enemies may have ecological (Maron and Vilà

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2001; Keane and Crawley 2002; Wolfe 2002; Liu and Stiling 2006 but see Parker and Hay 2005; Parker et al. 2006) and/or evolutionary responses in the introduced range (Thompson 1998; Mooney and Cleland 2001). The evolution of increased competitive ability (EICA) hypothesis proposes that invasive plants evolve reduced herbivory resistance and increased growth and/or reproduction because they are seldom attacked in introduced ranges (Blossey and Nötzold 1995). Nevertheless, tests of the EICA hypothesis have produced inconsistent results (Bossdorf et al. 2005).

While the EICA hypothesis postulates the successful invasion of exotic plants as an evolutionary response to decreased herbivory resistance, herbivory defense may involve both resistance (traits that reduce herbivory damage), and tolerance traits (traits that buffer the negative fitness impacts of herbivory damage; van der Meijden et al. 1988; Tiffin 2000; Müller-Schärer et al. 2004). Ecological theory predicts a trade-off between resistance and tolerance, suggesting that reduced herbivory resistance may translate into increased tolerance to herbivory (Strauss and Agrawal 1999; Stowe et al. 2000; Stastny et al. 2005). According to the EICA hypothesis, natural selection will favor fast-growing traits of invasive plants as a response to low levels of herbivory, which eventually leads to genetic shifts in growth traits between native and invasive populations (Bastlová and Květ 2002; Erfmeier and Bruelheide 2005; Güsewell et al. 2006; Zou et al. 2007). By virtue of these new traits, invasive plants would also be expected to have greater compensative ability following herbivory damage. As a consequence, invasive plants may evolve to be faster growing, less herbivore-resistant, and more herbivore-tolerant. To our knowledge, however, no study has simultaneously examined competitive ability, herbivore resistance, and tolerance of genotypes of invasive plants.

While most EICA studies have been conducted in the introduced range, common garden studies are increasingly being established in the native range (Leger and Rice 2003; Bossdorf et al. 2004a; Wolfe et al. 2004; Meyer et al. 2005). In previous common garden EICA studies, on the other hand, performances of native and invasive populations were compared without competition (Willis and Blossey 1999; Willis et al. 2000; Wolfe et al. 2004), or with interspecific competition against other species (Leger and Rice 2003; Vilà et al. 2003). However, exotic plants encounter different sets of competitors in their native and introduced ranges and they may be adapted to some extent to their native ones (Callaway and Aschehoug 2000; Hierro et al. 2005). Thus, interspecific competitors from only one distributional range might give a biased picture (Bossdorf et al. 2004a, 2005). Recently, a common garden study in which plants from native and invasive populations compete against each other has been suggested as an effective approach for testing the EICA hypothesis (Bossdorf et al. 2005).

Results of studies on *Sapium sebiferum* in the introduced range generally support the EICA hypothesis. Performances of native and invasive populations of *S. sebiferum* were compared in the presence of herbivores in the introduced range (Siemann and Rogers 2001, 2003a, b; Siemann et al. 2006) or with simulated herbivore damage (Rogers and Siemann 2004, 2005). However, simulated herbivory may not adequately mimic real insect damage in the native range (van Kleunen and Schmid 2003; Meyer et al. 2005). Simulated herbivory may also show a biased measurement of herbivory tolerance (Strauss and Agrawal 1999). If a species experiences different enemy regimes in different ranges, study outcome may differ between native and introduced ranges (van Kleunen and Schmid 2003; Wolfe et al. 2004; Meyer et al. 2005). Thus, experiments in native and introduced ranges are necessary to compare the performance and herbivore susceptibility between native and invasive populations (Maron et al. 2004; Wolfe et al. 2004; Bossdorf et al. 2005; Hierro et al. 2005).

Performance of invasive plants and their ability to compensate for leaf damage are strongly influenced by availability of soil resources (Davis et al. 2000; Elberse et al. 2003). A previous common garden study in the introduced range found that the competitive success of *S. sebiferum* seedlings from native and invasive populations was independent of nutrient addition when they competed against ryegrass *Lolium multiflorum* (Rogers and Siemann 2004). When seedlings from native and invasive populations of *S. sebiferum* are grown together in the presence of herbivores in the native range, whether the outcome of their intraspecific competition depends on soil fertility is unknown.

Compared with the previous *S. sebiferum* studies testing the EICA hypothesis, the approach of this study differs in four aspects: First, this common garden pot experiment was performed in the presence of natural herbivores from *S. sebiferum*'s native range of China. Second, we examined their differences in tolerance to herbivory in the native range rather than using simulated herbivory damage. Third, this study primarily focused on the intraspecific competition between native and invasive populations of *S. sebiferum* instead of interspecific competition. Finally, we discriminated among different populations within each continent to examine their differences in relative performance and herbivore susceptibility.

The main objective of this study was to test the EICA hypothesis by comparing the performance of native and invasive populations of *S. sebiferum* when plants from southern and northern populations in the native Chinese range and from Texas and Georgia populations (USA) in the invasive range were grown in all pairwise combinations in the presence of natural herbivores from the native Chinese range. Specifically, we addressed the following questions: (1) Do plants from invasive populations outperform those from native populations when they are grown in monoculture and mixture? (2) Are herbivore susceptibility and tolerance to herbivory of invasive populations greater than those of native populations? (3) Does performance of plants from different populations within each continent differ? (4) Does the outcome of intraspecific competition or relative performance depend on fertilizer addition?

Materials and methods

Study species

Chinese tallow tree (*S. sebiferum* L. Roxb., Euphorbiaceae, synonyms include *Triadica sebifera*) is native to China, where it occurs naturally and has been cultivated for fourteenth centuries (Zhang and Lin 1994). *S. sebiferum* was first introduced to Georgia, United States, in the late eighteenth century from Asia for agricultural purposes and later to Texas by the United States government in the early twentieth century (Bruce et al. 1997). Currently, Chinese tallow tree has become a severe invader that aggressively displaces native plants and forms monospecific stands in the southeastern USA (Bruce et al. 1997; Siemann and Rogers 2003c).

Seeds

In November and December 2003, seeds were hand collected from populations of naturalized *S. sebiferum* trees in Texas (TX) and Georgia (GA) states, USA, and in southern (CS, covering Guangdong, Fujian, and Jiangxi provinces in China) and northern China (CN, covering Jiangsu, Anhui, and Zhejiang provinces in China) populations of *S. sebiferum* (Table 1). Seeds were collected from 4 to 20 different trees at each site. Texas and Georgia populations represent places of first and later separate introductions, respectively. These two populations have been documented to be likely from different sources in China (DeWalt et al. 2006; S. J. DeWalt et al., unpublished data), and thus they were treated as distinct *S. sebiferum* invasive populations in this study. Seeds from Jiangsu, Anhui, and Zhejiang provinces (30–32°N) and from Guangdong, Fujian, and Jiangxi provinces (23–26°N) represent the northmost and southmost distribution areas of *S. sebiferum* in China mainland, respectively. Plants from different provinces within southern or northern area likely experience similar climates (Zhang and Lin 1994), while northmost and southmost populations were separated by hundreds of miles. A previous laboratory study found no significant difference in *S. sebiferum* seedling performance or herbivore damage between populations from Fujian and Guangdong provinces (Siemann and Rogers 2003a). Thus, seeds from different provinces within each distribution area of *S. sebiferum* in China were treated as one population for this study (Table 1).

Seeds of both native and introduced *S. sebiferum* trees were separately planted in 50-ml cone-tainers$^{\text{TM}}$ (Stuewe and Sons, Corvallis, OR, USA) in an unheated shadehouse at Nanjing Agricultural University, Nanjing, Jiangsu, China (32°2′N, 118°50′E) in December 2003. Soil was taken from the top 20 cm of the profile in fields at Jiangsu Academy of Agricultural Sciences in Nanjing where *S. sebiferum* trees are naturalized in uncultivated areas, although using soil from one location where seeds were collected could have affected the outcome of experiments. Planted seeds remained dormant throughout the winter season and germinated during March 2004.

Table 1 Native (China) and invasive (USA) populations of *Sapium sebiferum* that were used in this study

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

CN and CS represented northern and southern areas of *S. sebiferum*'s natural distribution in China, respectively. TX and GA represented Texas and Georgia states of USA, respectively

The small seedlings grew in the cone-tainers for about 4 weeks until they had secondary leaves, at which time they were transplanted into 6.50-l tree pots. 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 (Jones and McLeod 1990; Bruce et al. 1997). Thus, this study used first-year *S. sebiferum* seedlings to test the EICA hypothesis. To minimize maternal effects due to differences in seed qualities, seedlings of similar height and number of leaves without insect damage were selected for the pot experiments in this study.

Experimental design

A common garden pot experiment was performed in the screenhouse at Nanjing Agricultural University, Jiangsu, China, where several *S. sebiferum* trees were growing in the surrounding vicinity. This screenhouse was surrounded by coarse wire mesh that limited access to birds and mammals but allowed access to insects, mollusks (e.g., snails), and precipitation. At the beginning of May 2004, seedlings of similar height and number of leaves from native and invasive populations were combined to form all pairwise combinations (TX–TX, GA–GA, CN–CN, CS–CS, TX–GA, CN–CS, TX–CN, TX–CS, GA–CN, and GA–CS). Each pair was transplanted into a 6.5-l tree-pot filled with topsoil from the fields surrounded by natural *S. sebiferum* trees. To test the effect of soil fertility on seedling performance and on the outcome of competition, half of the pots received nitrogen fertilizer that was applied as urea at the rate of 6 g pot^{-1} just before seedling transplanting. Pots with no nitrogen addition served as controls. In total, 120 pairs of seedlings from native and introduced ranges were planted in a full-factorial design (ten pair types × 2 fertility levels) with six replicates. The pots were randomly arranged, watered as needed and re-randomized biweekly during the course of the experiment. All seedlings survived until the end of experiment on August 29, 2004.

Based on whether paired seedlings in one pot were from the same continent or from different continents, the experiment was divided into two sub-experiments for analyses. In one sub-experiment ("single continent sub-experiment"), a pair of seedlings from the same continent (TX–TX, GA–GA, TX–GA, CS–CS, CN–CN, and CS–CN) was used to test the effects of fertilizer and the origin of continent on performance of native and invasive populations. We also compared the performance of seedlings from different populations within each continent (TX–TX versus

GA–GA or CS–CS versus CN–CN). The pair of seedlings of TX–GA or CN–CS was used to examine the differences in competitive ability and herbivore susceptibility between populations within each continent. In a second sub-experiment ("mixed continent sub-experiment"), the seedlings in each pot were from different continents (TX–CS, TX–CN, GA–CS, and GA–CN). This sub-experiment was designed to compare the competitive ability of *S. sebiferum* seedlings from invasive populations relative to native populations with or without nitrogen addition.

Data collection

We measured stem height and recorded the number of leaves on each seedling on April 30 prior to initiation of experiment. Before plant harvesting, we took a final measurement of stem height from ground surface to the terminal bud and recorded the total number of leaves and average percentage of surface area damaged per leaf. Percent leaf damage was measured using a computer program ScnImage (Siemann and Rogers 2003a). On August 29, shoots of each seedling were harvested, dried at 60°C for 3 days and weighed separately. We did not measure root mass since it is difficult to accurately partition the roots from different plants within one pot. Stem height increment was calculated as [(final height–initial height)/initial height]. Percent defoliation of leaf surface area was square-root transformed for analysis.

Statistical analyses

In the "single continent sub-experiment," we used a two-way factorial analysis of variance (ANOVA) to test whether average shoot mass, stem height increment, number of leaves, or percent leaf defoliation of each pot depended on origin (continent), fertilizer or their interaction (TX–TX, GA–GA and TX–GA versus CS–CS, CN–CN and CS–CN, Table 1). We also performed a two-way ANOVA within each continent to examine the difference in average performance of each pot between populations (TX–TX versus GA–GA, or CS–CS versus CN–CN) as affected by fertilizer. A paired *t*-test was used to examine which population was more competitive than the other within each continent (TX–GA or CS–CN), and one-way ANOVA was used to examine whether the outcome of competition within each continent (difference between paired seedlings in each pot) was dependent on fertilizer addition. Thus, the Bonferroni-adjusted critical value for three non-independent comparisons was $\alpha = 0.017$. The true critical alphas for the tests are somewhere between $\alpha = 0.017$ and the adjusted alphas (Maxwell and Delaney 1990; García 2004). In the "mixed continent sub-experiment," we determined whether invasive and native *S. sebiferum* populations differed in measures of competitive ability or herbivore damage with a paired *t*-test (TX–CS, TX–CN, GA–CS, and GA–CN) and whether this depended on fertilizer addition with one-way ANOVA.

Similar to fitness reaction norms of genotypes exposed to different damage levels (Strauss and Agrawal 1999; Stowe et al. 2000; Agrawal et al. 2004), herbivory tolerance was depicted by the slope of the regression of percent leaf damage on shoot biomass (Fig. 3). We conducted an ANCOVA on shoot biomass with continent as the main effect and percent leaf damage as the covariate. Difference in tolerance between the two continent types was interpreted as a significant interaction (difference in regression slope). All statistical analyses were carried out using the JMP statistical software, Version 5.1 (SAS Institute, Cary, NC, USA).

Results

In the "single continent sub-experiment," fertilizer addition increased shoot mass, stem height increment, and number of leaves per seedling, but had no significant effect on leaf damage of seedlings from both native and invasive populations (Fig. 1, Table 2). The lack of a significant interaction of fertilizer with continent suggested a similar response of seedlings from invasive and native populations to fertilizer addition (Fig. 1, Table 2). Compared to native populations, seedling shoot mass was significantly higher, and leaf damage tended to be greater for seedlings from invasive populations than those from native populations (Fig. 1a, b, d, Table 2, term "Continent"). However, the differences in stem height increment and total number of leaves per seedling were not significant between native and invasive populations (Fig. 1b, Table 2).

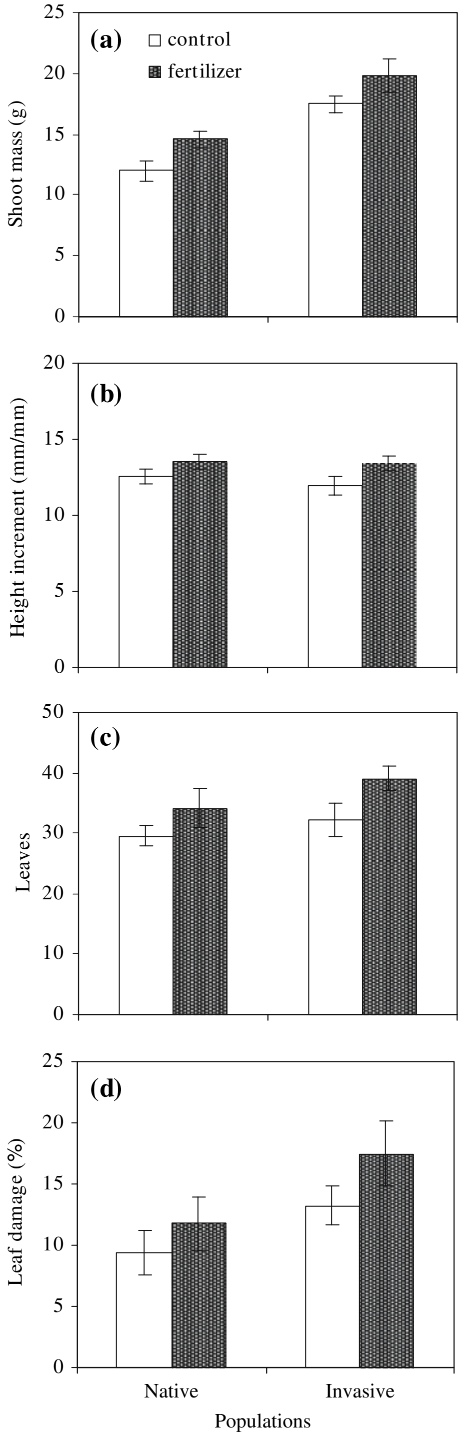

Fig. 1 Mean (±1 SE, $n = 18$) shoot mass (**a**), stem height increment (**b**), the number of leaves per seedling (**c**), and the percent leaf defoliation per seedling (**d**) of *Sapium sebiferum* from native and invasive populations in relation to fertilizer. Data were collected at the end of "single continent sub-experiment." Statistical analysis see Table 2

Shoot mass was significantly lower for both seedlings from invasive and native populations in the "mixed continent sub-experiment" (invasive populations: 13.60 ± 0.58 g pot^{-1}, native populations: 10.16 ± 0.67 g pot^{-1}) than in the "single continent sub-experiment'' (invasive populations: 17.52 ± 0.65 g pot^{-1}, native populations: 13.32 ± 0.54 g pot^{-1}), suggesting intraspecific competition between two population types ($P < 0.01$). Total number of leaves per seedling and leaf damage tended to be greater, and shoot mass was significantly higher for seedlings from the invasive population relative to the native population in the "mixed continent sub-experiment" [Fig. 2, Table 3, term "Native–Invasive (mixed continent)"]. Stem height increment of *S. sebiferum* seedlings from native and invasive populations did not significantly differ when they were competing against each other (Fig. 2, Table 3). Moreover, the outcomes of intraspecific competition between plants from native and invasive populations (Fig. 2) were not significantly affected by fertilizer addition ($F_{1,46} = 0.01$–2.02, $P = 0.16$–0.92).

When plants from different populations within the invasive range were competing against each other, shoot mass, stem height increment, total number of leaves, and leaf damage of *S. sebiferum* seedlings were not significantly different between TX and GA populations [Table 3, term "TX–GA (mixed population)"]. Also, no significant difference in competitive ability between CS and CN populations was found when they were competing against each other, except that herbivory damage per leaf was generally lower for the CS population than the CN population [Table 3, term "CS–CN (mixed population)"]. The outcome of competition between TX and GA was not affected by fertilizer addition ($F_{1,10} = 0.01$–1.61, $P = 0.11$–0.91). Differences in shoot mass, height increment, total number of leaves, and leaf damage between CS and CN populations were also independent of fertilizer addition ($F_{1,10} = 1.05$–2.46, $P = 0.15$–0.56).

When the pair of plants in each pot was from the same population within the invasive range [Table 3, term "TX–GA (single population)"], no significant differences in performance and herbivore damage per seedling were found between seedlings from TX and GA populations. The interactive effect of population with fertilizer on seedling performance was not significant ($F_{1,20} = 0.07$–0.53, $P = 0.22$–0.80). For

Table 2 A two-way ANOVA for effects of fertilizer and continent (seed origin) on performance of *Sapium sebiferum* in the "single continent sub-experiment"

Source	*df*	Shoot mass			Height increment			Total leaves			Leaf damage		
		SS	F	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Fertilizer	1	0.1	7.6	0.007	45	10.2	0.002	199	6.5	0.01	0.2	2.1	0.15
Continent	1	0.4	38.7	<0.0001	2	0.5	0.47	97	3.2	0.08	0.4	4.6	0.03
Fertilizer × continent	1	0.0	0.9	0.34	4	0.9	0.33	10	0.3	0.57	0.0	0.0	0.91
Model	3	0.5	15.8	<0.0001	51	3.9	0.01	305	3.3	0.02	0.6	2.3	0.09
Error	68	0.8			299			2,076			5.7		

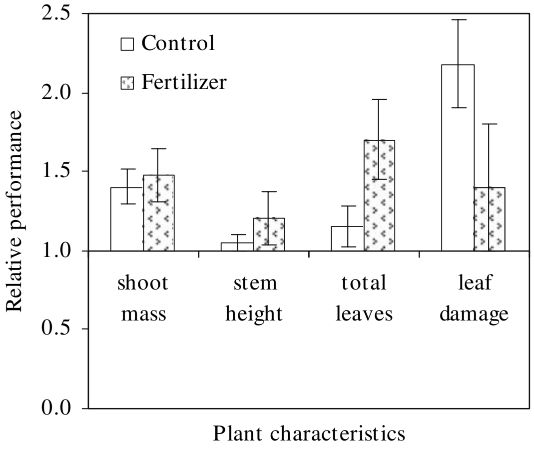

Fig. 2 Performance of *Sapium sebiferum* from the invasive population relative to the native population when they were competing against each other. The performance (shoot mass, stem height increment, leaves, and leaf damage) of *Sapium sebiferum* from the native population was standardized as "1." Data were collected at the end of "mixed continent sub-experiment." *Error bars* represent ±1 SE ($n = 24$). Statistical analysis see term "Native–invasive (mixed continent)" in Table 3

the pair of CS–CS versus CN–CN [Table 3, term "CS–CN (single population)"], on the other hand, shoot mass, stem height increment, total leaves, and leaf damage did not significantly differ between southern and northern populations. In addition, no interactions between population and fertilizer were found for *S. sebiferum* seedling shoot mass, stem height increment, total leaves, and percent of damage area per leaf ($F_{1,20} = 0.01$–0.55, $P = 0.44$–0.91).

In the regression analysis (Fig. 3), we did not discriminate between populations within each continent (TX versus GA or CS versus CN) because they did not significantly differ in growth and herbivore damage (see above, Table 3). Since no significant interaction of fertilizer with genotype was found on seedling performance in the "single continent sub-experiment" (Fig. 1, Table 2) or on the outcome of intraspecific competition in the "mixed continent sub-experiment" (Fig. 2), both fertilizer and control treatments data were included in regression analysis. A significant difference in the slope of regression for shoot biomass versus percent leaf damage showed that plants from native and invasive populations of *S. sebiferum* differed in tolerance to herbivory damage when they were grown in monoculture (interaction term: $P = 0.05$) and in mixture (interaction term: $P = 0.08$, Fig. 3). When they were grown in the native range, plant growth of the invasive populations was not significantly reduced with increasing herbivory damage [test of the regression slope differs from zero: $r^2 = 0.04$, $P = 0.15$ (a) and $r^2 = 0.05$, $P = 0.13$ (b)]. In contrast, a substantial reduction in growth with increasing herbivory damage was found for plants from the native populations of *S. sebiferum* [$r^2 = 0.21$, $P < 0.01$ (a) and $r^2 = 0.13$, $P = 0.02$ (b), Fig. 3].

Discussion

Invasive populations outperformed native populations

The EICA hypothesis states that invasive plants evolve a reduction in herbivore resistance and an increase in growth in response to low herbivory in their introduced range (Blossey and Nötzold 1995). Compared with native populations, we found that shoot mass was significantly greater for invasive populations in both sub-experiments. Total number of

Table 3 Statistical analyses for differences in performance and herbivore damage of *Sapium sebiferum* seedlings from two continents (Native–invasive, paired *t*-test) in the “mixed continent sub-experiment,” or from two different populations (mixed population in one pot: TX–GA or CS–CN, paired *t*-tests or single population in one pot: TX–TX versus GA–GA, CS–CS versus CN–CN, ANOVAs) in the “single continent sub-experiment”

Seedling pairs	*df*	Shoot mass		Height increment		Total leaves		Leaf damage	
Native–invasive (mixed continent)	47	$t = 3.56$	$P = 0.0009$	$t = 0.75$	$P = 0.45$	$t = 2.14$	$P = 0.04$	$t = 1.86$	$P = 0.07$
TX–GA (mixed population)	11	$t = 1.56$	$P = 0.15$	$t = 1.21$	$P = 0.25$	$t = 0.73$	$P = 0.48$	$t = 1.05$	$P = 0.31$
CS–CN (mixed population)	11	$t = 0.44$	$P = 0.67$	$t = 1.07$	$P = 0.31$	$t = 0.42$	$P = 0.86$	$t = 2.15$	$P = 0.06$
TX–GA (single population)	1, 20	$F = 3.89$	$P = 0.06$	$F = 0.01$	$P = 0.91$	$F = 1.50$	$P = 0.23$	$F = 4.22$	$P = 0.05$
CS–CN (single population)	1, 20	$F = 0.79$	$P = 0.38$	$F = 2.87$	$P = 0.11$	$F = 1.48$	$P = 0.24$	$F = 0.98$	$P = 0.33$

leaves per seedling and herbivory damage tended to be greater for invasive populations than native populations. Thus, the results of this study are consistent with the EICA hypothesis prediction and the previous results in introduced ranges, suggesting that *S. sebiferum* has evolved to be a faster-growing and less herbivore-resistant plant in response to low-herbivore loads in its introduced range (Siemann and Rogers 2001, 2003a, b; Rogers and Siemann 2004, 2005). Greater growth and more herbivore damage to plants from invasive populations than native populations when grown in the presence of enemies from the native range were also found in *Silene latifolia* by Wolfe et al. (2004) and in *Senecio jacobaea* by Stastny et al. (2005).

Greater tolerance of invasive populations relative to native populations

In addition to herbivory resistance, invasive species may also evolve herbivory tolerance as a feature of fast-growing plants (van der Meijden et al. 1988; Strauss and Agrawal 1999; Stowe et al. 2000; Tiffin 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. The regressions of leaf damage on growth in this study indicated that growth of the native populations was significantly decreased by herbivory, while there was no pronounced impact of herbivory on that of invasive populations. Greater compensative ability of invasive populations relative to native populations was also found when they experienced simulated root damage (Rogers and Siemann 2004) or simulated leaf removal of 50% (Rogers and Siemann 2005). These results suggest that plants from invasive populations of *S. sebiferum* tolerate herbivory more efficiently relative to those from native populations. In Hawaii, however, *S. sebiferum* from North American populations receives very high amounts of damage from introduced Asia beetles, and *S. sebiferum* from Asia populations receives less damage and grow faster (Siemann and Rogers 2003b).

Currently recognized mechanisms underlying herbivore tolerance include plant traits such as relative growth rate, biomass allocation pattern, plant photosynthetic rate, and nutrient use efficiency (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999; Stowe et al. 2000; Tiffin 2000). These effective herbivore tolerance mechanisms could be common in invasive plants (Müller-Schärer et al. 2004). 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 they were competing with other species (e.g., Pattison et al. 1998; Smith and Knapp 2001; Grotkopp et al. 2002; McDowell 2002) or with their conspecifics from their native ranges (e.g., Bastlová and Květ 2002; Buschmann et al. 2005; Erfmeier and Bruelheide 2005; Güsewell et al. 2006). In previous common garden studies, we found that plants from invasive populations relative to native populations of *S. sebiferum* exhibited higher relative growth rates associated with lower ratios of root to shoot, higher photosynthetic rates, and greater total leaf area (Zou et al. 2006, 2007). At the time of leaf damage, growth of plants with low root-shoot ratios and large leaf area is expected to be less affected by herbivory (Tiffin 2000). These genetic shifts in traits may have given rise to their capacity to regrow after herbivore damage, and thus increase their herbivory tolerance.

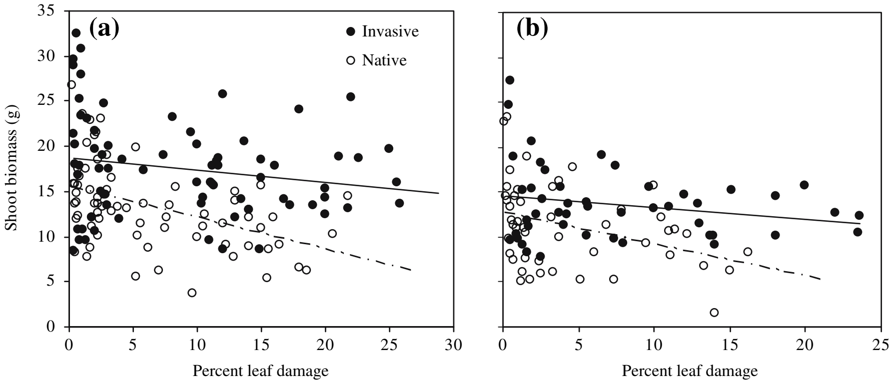

Fig. 3 Regression of shoot biomass against percent leaf damage for native and invasive populations of *Sapium sebiferum* when they were grown in monoculture (**a**) and mixture (**b**). Slopes for the regression lines. Native populations: −0.3532 (**a**) and −0.3535 (**b**); invasive populations: −0.1299 (**a**) and −0.1247 (**b**)

Although herbivory tolerance has received little attention in the context of plant invasion, a trade-off between resistance and tolerance has important implications for biological control on invasive plants (Bossdorf et al. 2004b; Müller-Schärer et al. 2004; Rogers and Siemann 2004, 2005; 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 populations of biological control agents would be high-over extended time periods because they are not affected by tolerance as strongly as resistance. Unfortunately, comparisons of herbivore tolerance between native and invasive populations have been largely neglected, and very few studies have examined shifts in intrinsic traits that are considered fundamental mechanisms for herbivore tolerance of invasive plants. Certainly, these studies deserve to be strengthened in the future.

No significant difference in performance between populations within each continent

When grown in monoculture or mixture, *S. sebiferum* performance did not significantly differ between southern and northern Chinese populations, or between Texas and Georgia populations (Table 3). Similarly, a previous pot study showed no significant performance differences between Chinese provincial populations of *S. sebiferum* (Siemann and Rogers 2003a). Although a long-term field common garden study found that some genetic differences existed between trees from Texas and Georgia populations, the difference in leaf damage between trees from Texas and Georgia populations was not significant (Siemann and Rogers 2001). Moreover, the individual tree performances were measured in the 14th year in their study. In contrast, this study addressed the competitive ability of *S. sebiferum* seedlings using a 4-month common garden pot experiment in the native range. Overall, performance differences between populations from the same continent were comparatively minor, whereas differences between populations from different continents were very significant in this study.

Outcomes of intraspecific competition independent of fertilizer addition

In the present study, the outcome of competition between native and invasive populations was independent of fertilizer addition. Also, no significant interaction between fertilizer and origin of continent was found in the “single continent sub-experiment,” although fertilizer addition increased shoot mass, stem height, and total leaves of plants for both native and invasive populations. Similar to the results of this study, Rogers and Siemann (2004) found that fertilizer addition increased the performance of both native and invasive populations of *S. sebiferum*, but the competitive success [*S. sebiferum* shoot mass/(*S. sebiferum* shoot mass + grass shoot mass)] of *S. sebiferum* seedlings was independent of nutrient addition when *S. sebiferum* competed against ryegrass *L. multiflorum*.

Competition-free versus competition studies

Relative performance of *S. sebiferum* seedlings in the “single continent sub-experiment” was consistent with the outcome of intraspecific competition in the "mixed continent experiment." However, Leger and Rice (2003) found more rapid growth and greater herbivore susceptibility of invasive populations relative to native populations of California poppies (*Eschscholzia californica*) only when the plants were grown without competitors. Recently, a study with *Alliaria petiolata* showed that under optimal, competition-free conditions there were no differences in fitness between native and invasive populations (Bossdorf et al. 2004a). When plants were competing against conspecifics, in contrast, native populations outperformed invasive populations. Therefore, they challenged some previous EICA tests in which performance of native and invasive populations were compared in competition-free environments (Willis and Blossey 1999; Willis et al. 2000; Wolfe et al. 2004). Indeed, performance in the absence of competition may not predict competitive ability, for instance if the ability of a plant to rapidly exploit resources has a different mechanistic basis than its ability to tolerate low-resource levels (e.g., Grime 1979; Goldberg 1996).

Intraspecific competition versus interspecific competition studies

This study primarily focused on intraspecific competition instead of interspecific competition that has been used in the recent tests of the EICA hypothesis. Vilà et al. (2003) found no difference in competitive ability between native and invasive *Hypericum perforatum* when they competed against a native grass. However, interspecific competitors from only one distributional range might give a biased picture (Bossdorf et al. 2004a, 2005). In the previous study in which native and invasive populations of *S. sebiferum* separately competed with ryegrass *L. multiflorum*, for example, plant mass of both were unaffected by ryegrass presence, and hence the competitive outcome did not differ between them (Rogers and Siemann 2004). In this study, however, the outcome of intraspecific competition revealed that regardless of nitrogen condition, invasive populations were more competitive than native populations. Exotic plants encounter different sets of competitors in their native and introduced ranges and they may be adapted to some extent to their native ones (Callaway and Aschehoug 2000; Hierro et al. 2005). In contrast, the outcome of intraspecific competition between native and invasive populations could be directly used to test the EICA hypothesis, and thus it deserves to be given more attention in future EICA studies (Bossdorf et al. 2005).

Native range versus introduced range studies

Higher growth and more herbivore susceptibility of invasive populations relative to native populations found in this study are generally consistent with the previous *S. sebiferum* studies conducted in the introduced range (Siemann and Rogers 2001, 2003a, b; Rogers and Siemann 2004). Wolfe et al. (2004) also found that the differences in life-history between *S. latifolia* plants from native and invasive populations in a common garden study in the native range were closely consistent with the results of a corresponding common garden experiment in the introduced range (Blair and Wolfe 2004). In contrast, Meyer et al. (2005) conducted a 2-year common garden study in the native range using *Solidago gigantea* and found invasive populations had higher enemy susceptibility and benefit more from insect removal than native populations, which is inconsistent with the result of common garden study that was performed in the introduced range by van Kleunen and Schmid (2003). One possible reason for this contradiction was that leaf herbivory simulated by van Kleunen and Schmid (2003) was not an adequate mimic of real insect damage in its native range. Only a sub-set of the insects were leaf chewers, and the sap-feeders, gap-makers, and leaf-miners were also found in the native range (Meyer et al. 2005). Similarly, we found both mollusks (e.g., the generalist Asian trampsnail, *Bradybaena similaris*) and insects (e.g., the specialist beetle species, *Bikasha collaris*) consuming *S. sebiferum* leaves in this study. Compared to natural herbivory conditions in the native range, however, the screenhouse limited access to some predators (e.g., birds and mammals), which may represent a limitation of this study.

Indeed, the EICA hypothesis prediction was primarily based on the assumption that invasive plants are mostly released from specialist herbivores in their introduced range (Blossey and Nötzold 1995; Memmott et al. 2000; Keane and Crawley 2002; DeWalt et al. 2004). Unfortunately, a generalist herbivore in the introduced range was often introduced to test the

EICA hypothesis in most previous studies, while only few common garden studies have been performed in the native range. Because resistances against specialists and generalists are likely based on different mechanisms (van der Meijden 1996; Müller-Schärer et al. 2004; Joshi and Vrieling 2005; Leger and Forister 2005; Müller and Martens 2005), studies that address both simultaneously may find different results (Bossdorf et al. 2005). Therefore, a common garden study focusing on intraspecific competition between native and invasive populations in the presence of natural enemies from the native range could be a strong approach for testing the EICA hypothesis.

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