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Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore

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Abstract Invasive plants are often larger in their introduced range compared to their native range. This may reflect an evolved reduction in defense and increase in growth in response to low herbivory in their introduced range. Key elements of this scenario include genetic differences in defense and growth yet uniformly low rates of herbivory in the field that dissociate defense and herbivore damage for alien species. We conducted a laboratory experiment with *Melanoplus angustipennis* grasshoppers and Chinese Tallow Tree seedlings (*Sapium sebiferum*) from its native range (China) and its introduced range (Texas, USA) where it is invasive. We caged grasshoppers with pairs of *Sapium* seedlings from the same continent or different continents. The amounts of leaf area removed from Texas and China seedlings, and their height growth rates, were indistinguishable when both seedlings in the pair were from the same continent. However, when grasshoppers had a choice between seedlings from different continents, they removed more Texas *Sapium* foliage than China *Sapium* foliage and height growth rates were higher for China *Sapium* seedlings compared to Texas seedlings. Grasshopper growth rates increased with greater *Sapium* foliage consumption. In a common garden in Texas, *Sapium* seedlings from Texas grew 40% faster than those from China. Chewing insect herbivores removed little *Sapium* foliage in the field experiment. Although grasshoppers preferred to feed on Texas *Sapium* when offered a choice in the laboratory, extremely low herbivory levels in the field may have allowed the Texas seedlings to outperform the China seedlings in the common garden. These results demonstrate post-invasion genetic differences in herbivore resistance and growth of an invasive plant species together with a decoupling of defense and herbivore choice in the introduced range.

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Introduction

Some invasive plants are more vigorous in their introduced range compared to their native range (Elton 1958; Crawley 1987; Blossey and Nötzold 1995; Mack et al. 2000; but see Thebaud and Simberloff 2001). Insect herbivores may contribute to this fact because invasive plants frequently have low losses to herbivores in their introduced range (Elton 1958; Lodge 1993; Yela and Lawton 1997). This may influence plant vigor in two different ways. First, resources normally lost to enemies or production of defenses may be allocated to growth and/or reproduction by a plastic phenotypic response ("Enemies Hypothesis" or "Enemy Release Hypothesis"; Bazzaz et al. 1987; Tilman 1999; Alpert et al. 2000; Thebaud and Simberloff 2001; Keane and Crawley 2002). Alternatively, invasive plants may evolve reduced allocation to defense and increased allocation to growth and/or reproduction because they are seldom attacked by enemies ("Evolution of increased competitive ability hypothesis" or "EICA"; Blossey and Nötzold 1995). Because allocation to defense may be as costly as herbivore damage (Bazzaz et al. 1987; Simms and Rausher 1987), plants that escape their enemies in an introduced range would gain a selective benefit from decreasing their defensive investment.

The EICA hypothesis makes several testable predictions. First, invasive genotypes (i.e. from the introduced range) should have greater growth and/or reproduction than native genotypes (i.e. from the native range) when they are grown in a common garden (Blossey and Nötzold 1995; Willis and Blossey 1999; Willis et al. 2000; Siemann and Rogers 2001). Second, invasive genotypes should have lower herbivore defenses than native genotypes in a common garden (Siemann and Rogers 2001). Third, herbivores in the introduced range should avoid or feed lightly on all varieties of the alien plant in field conditions, thereby dissociating defense from damage for alien species (Siemann and Rogers 2001). Fourth, native genotypes should have higher resistance to herbivores from their native range compared to that of invasive genotypes (Daehler and Strong 1997). Finally, although herbivores in the introduced range avoid feeding on the introduced plant in natural conditions, they should prefer less defended invasive genotypes in controlled feeding trials. If the combination of reduced defense, high growth rates and low losses to herbivores contributes to the invasive genotype's success in the introduced range, overcoming the behavioral avoidance of herbivores in artificial environments may remove the advantage of invasive genotypes.

In many areas of the southeastern United States, the introduced Chinese Tallow Tree [*Sapium sebiferum* (L.) Roxb., Euphorbiaceae, "*Sapium*" hereafter] aggressively displaces native plants and forms monospecific stands (Bruce et al. 1997; Siemann and Rogers 2003). *Sapium* is native to Asia where it occurs naturally and has been cultivated for 14 centuries (Bruce et al. 1997). *Sapium* was purposely introduced to Georgia in the late eighteenth century from Asia for agricultural purposes and later to Texas, Florida and Louisiana by the United States government in the early twentieth century (Bruce et al. 1997). A 14-year common garden experiment in Texas with *Sapium* genotypes from Asia and North America showed lower concentrations of defense chemicals in the foliage of mature trees (tannins) and higher growth rates for North American genotypes compared to those from Asia (Siemann and Rogers 2001). Despite differences in defense and foliage quality, mature trees of all genotypes suffered low levels of chewing insect herbivory (0.25% of leaf area).

Melanopline (Orthoptera: Acrididae: Melanoplinae) grasshoppers are generalist feeders that typically consume a mixed diet of forbs, woody plants and grasses (Ueckert and Hansen 1971). They are able to consume forbs and woody plants that contain a variety of defensive compounds by detoxifying them (Majak et al. 1988) or allowing them to pass harmlessly through the digestive tract (Ehmke et al. 1989). The most abundant species in this subfamily in coastal East Texas tallgrass prairie is the narrow-winged sand grasshopper, *Melanoplus angustipennis* Dodge (unpublished data). They are sometimes extremely abundant in Colorado and Nebraska grasslands as well (Alexander and Hilliard 1969; Joern 1982). They have been documented to consume over 35 species of plants, with a greater proportion of their diet being forbs and woody plants than grasses (Ueckert and Hansen 1971).

We performed a laboratory experiment to investigate whether *M. angustipennis* grasshoppers preferred to eat native or invasive genotype *Sapium* seedlings and how these feeding choices impacted growth rates of both grasshoppers and seedlings. We performed a field experiment with the same genotypes of *Sapium* to examine their growth in a more natural setting where the same species of grasshopper is abundant but was not manipulated.

Materials and methods

Seeds

In December 2000, seeds were hand collected from *Sapium* trees in the Houston metropolitan area (Galveston and Harris counties, Texas; "TX" seeds hereafter). Since the Texas collecting areas were in close proximity they were treated as a single area in the experimental design and analysis. During this same time, seeds were hand collected from *Sapium sebiferum* trees in the Guangdong ("$\mathrm{CH_G}$" hereafter) and Fujian ("$\mathrm{CH_F}$" hereafter) provinces of China. Seeds were quarantined in China to check for pests and then shipped by air freight to Houston in January 2001 and February 2001, respectively. These provinces span hundreds of miles and may represent distinct populations of *Sapium*. Each set of seeds were stored in the dark at room temperature until planting.

In February 2001, we planted each set of seeds in a separate greenhouse flat in an unheated greenhouse. The temperature oscillation in this environment effectively stimulates *Sapium* germination (Nijjer et al. 2002). Seeds for this experiment germinated throughout April. Each germinated seed was transferred to a conetainer (Stuewe and Sons, Corvallis, Ore, USA) filled with a mix of commercially available topsoil and humus.

Laboratory experiment set-up

At the beginning of June, we transferred pairs of seedlings into 48 9-l tree-pots filled with a mix of commercially available topsoil and humus. In one sub-experiment ("single continent sub-experiment") both seedlings in the pair were from the same continent (Fig. 1). This would only detect large differences in grasshopper feeding preferences (Capinera 1993). In a second sub-experiment ("choice sub-experiment") pairs of seedlings represented each continent (Fig. 1). This was designed to test for more subtle differences in grasshopper feeding preference (Capinera 1993).

We installed aluminum mesh cages in each tree-pot. These cages were cylinders of aluminum window screening (75 cm high, 300 cm^2, 1.6 mm mesh size aluminum) joined to aluminum flashing that was fitted 1 cm into the dirt in the pot. These cages were smaller versions of the cages used by other investigators in field experiments with grasshoppers (Ritchie and Tilman 1993; Schmitz 1994). We contacted O.J. Schmitz to insure that they were made from the same materials, assembled in the same fashion and installed with the same methods.

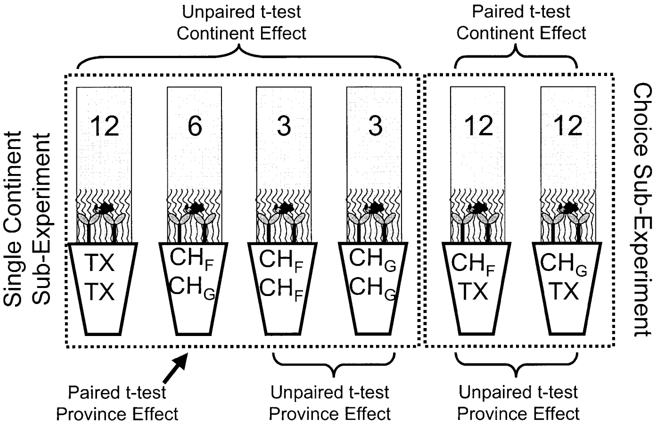

Fig. 1 Design of the laboratory experiment and statistical comparisons of leaf removal by grasshoppers and plant growth. Letters within pots designate the source of seeds for the pair of *Sapium* seedlings. (*TX* Texas, USA; CH_F Fujian, China; CH_G Guangdong, China. Numbers indicate the replicates for that pairing of seedling types)

Pots were placed in a temperature controlled (27°C) laboratory area. One wall of the room was mostly windows so the plants received abundant natural light. The natural light provided 530 μmol/m^2 per second of PAR on average across the experiment during peak light as measured by an ACCUPAR linear ceptometer (Decagon, Pullman, Wash., USA). Full spectrum lights suspended over the experiment provided an additional 85 μmol/m^2 per second of PAR on a 12 h light/12 h dark cycle. Measurements with a point quantum sensor (LICOR, Lincoln, Neb., USA) showed that the screen cages transmitted 60% of light as PAR. Overall, seedlings received the equivalent of approximately 20% of full sunlight. Pots were watered lightly every day and rotated in place. Because light or other factors may have varied across the experiment, pots were rotated among positions in the experiment twice per week.

Ten days after the seedlings were planted in the tree-pots, we planted gulf annual ryegrass seed (*Lolium multiflorum* Lam., Pennington Seed, Lebanon, Ore., USA) at the recommended rate of 50 g/m^2 (1.5 g per pot). Seeds were covered with 5 mm of topsoil. Within 2 days, seeds germinated and the grass was growing vigorously. The presence of grass allowed grasshoppers the choice of avoiding feeding on *Sapium* seedlings altogether.

Three days later, we caught adult individuals of *M. angustipennis* in tallgrass prairie at the University of Houston Coastal Center, Galveston County, Tex., USA. This research site is heavily invaded by *S. sebiferum* (Siemann and Rogers 2001). We haphazardly selected 48 male individuals that had all their legs and no visible injuries. These grasshoppers were starved for 24 h.

The next day, we measured the height of each *Sapium* seedling from ground surface to the terminal bud. We weighed grasshoppers to the nearest 0.1 mg and placed one grasshopper in each screen cage (day 0 henceforth).

Laboratory experiment data collection

Cages were checked daily for grasshopper survival. Grasshoppers that died in first 24 h were assumed to have died from handling stress and replaced with a new grasshopper that had been similarly starved and weighed (three of these: TX-TX, TX-TX, TX-$\mathrm{CH_F}$). During the course of the 14 day experiment, two grasshoppers escaped or died ($\mathrm{CH_F}$-$\mathrm{CH_F}$ day 9; $\mathrm{CH_G}$-TX day 13). We did not recover the body of either when we ended the experiment. These were counted as missing datapoints in the grasshopper growth rate analysis.

We visually inspected *Sapium* seedlings for chewing damage on days 4 and 7. Twenty grasshoppers had removed *Sapium* foliage by day 4 and 31 had done so by day 7. All combinations of seedling type and seedling pairs had experienced chewing by at least one of the grasshoppers by day 4 except $\mathrm{CH_F}$ seedlings in $\mathrm{CH_F}$-$\mathrm{CH_G}$ pots. Only one grasshopper ($\mathrm{CH_G}$-$\mathrm{CH_G}$) had not consumed any *Sapium* foliage by day 14.

On day 14, we removed the grasshoppers. We starved them for 24 h and then weighed them to the nearest 0.1 mg. We calculated growth rates as [(day 14 mass−day 0 mass)/day 0 mass]. Over the short time period of this experiment, this growth rate metric was nearly perfectly correlated with instantaneous growth rate [ln(day 14/day 0)] for grasshopper growth rates (r=0.999) and plant height growth rate (see below, r=0.998).

On day 14, we measured the heights of *Sapium* seedlings. Height growth rates were calculated as [(day 14 height−day 0 height)/day 0 height]. We removed their leaves, counted them and scanned them on a flatbed scanner. We measured average percent leaf area of each seedling removed by grasshoppers using the computer program NIH Image v.1.62 (available at http://rsb.info.nih.gov/nih-image/). This is the same method used in Siemann and Rogers (2001). The leaves were dried and weighed. We estimated the mass of leaves of each *Sapium* seedling eaten by grasshoppers as [(mass remaining)/(% leaf area remaining)×(% leaf area removed)]. We clipped the grass at ground level, dried it and weighed it.

Laboratory experiment analyses

We tested whether grasshopper growth rates in the full experiment depended on sub-experiment (choice vs single continent), continental pairings (CH-CH, CH-TX, TX-TX) and genotype combinations ($\mathrm{CH_F}$-TX, $\mathrm{CH_G}$-TX, TX-TX, $\mathrm{CH_F}$-$\mathrm{CH_G}$,$\mathrm{CH_F}$-$\mathrm{CH_F}$,$\mathrm{CH_G}$-$\mathrm{CH_G}$) using a sequential ANOVA (i.e. Type I SS). For all sequential ANOVAs we used SAS (v. 8.2, SAS, Cary, N.C., USA). In this type of analysis, later terms in the model explain residual variance only after accounting for the explanatory power of the earlier factors. We tested whether the estimated mass of *Sapium* foliage consumed differed among pots in the entire experiment using an analogous sequential ANOVA. We tested whether the mass of grass in the pots differed using a third sequential ANOVA with the same predictors.

We tested whether amount of foliage removed depended on continental origin of a seedling in the single continent sub-experiment using an unpaired t-test (Fig. 1). An unpaired test is appropriate when seedlings share a treatment but not a grasshopper or pot. We used another unpaired t-test to examine whether amount of foliage removed depended on provincial origin of Chinese seedlings when both seedlings in a pot were from the same province. We used a paired t-test to examine the effect of province when there was a Chinese seedling from each province in the pot. A paired test accounts for seedlings sharing a grasshopper and competing when they shared a pot. For all t-tests we used Statview (v. 5.0, SAS, Cary, N.C., USA). We tested whether the amount of foliage removed depended on continental origin of a seedling in the choice sub-experiment using a paired t-test (Fig. 1). We tested whether amount of foliage removed depended on the provincial origin of Chinese seedlings using an additional unpaired t-test. We performed an identical set of analyses for each sub-experiment substituting *Sapium* seedling height growth rate as the response variable.

We tested whether grasshopper growth rates and estimated mass of *Sapium* foliage consumed were correlated with a z-test (Statview). We did not use regression because there was an uncertain direction of causation with these two variables. We performed another correlation with grass mass and grasshopper growth rates. We used a simple regression (Statview) to test whether the height growth rates of *Sapium* seedlings depended on the percent of leaf area removed.

Field experiment

In May 2001, seedlings of the three genotypes (28 $\mathrm{CH_F}$, 28 $\mathrm{CH_G}$ and 35 TX) that had been growing in conetainers (see above) were planted with a 2 m spacing into a mowed field dominated by St. Augustine grass [*Stenotaphrum secundatum* (Walt.) Kuntze: Poaceae]. The grass was kept mowed throughout the growing season and the field was watered with soaker hoses whenever the soil was dry. Weed cloth suppressed background vegetation growth within 15 cm of seedlings and we hand weeded any plants that grew next to seedlings. The experiment was fenced to keep out feral hogs (*Sus scrofa* L.).

We measured seedling heights when they were transplanted (day 0) and again 139 days later in mid-October. At the later date, we also estimated the average percent of leaf area that had been removed by chewing insect herbivores. We used ANOVA to test whether height growth rate [(day 139 height−day 0 height)/day 0 height] depended on continental origin of seedlings (CH vs TX) and provincial origin of Chinese seedlings ($\mathrm{CH_F}$ vs $\mathrm{CH_G}$) in a sequential ANOVA. We performed an analogous ANOVA with chewing damage as the response variable.

Results

Grasshopper growth rates did not differ between sub-experiments ($F_{1,\,40}$=0.1, P=0.72) or between CH-CH and TX-TX pots ($F_{1,\,40}$=0.4, P=0.55) in the single continent

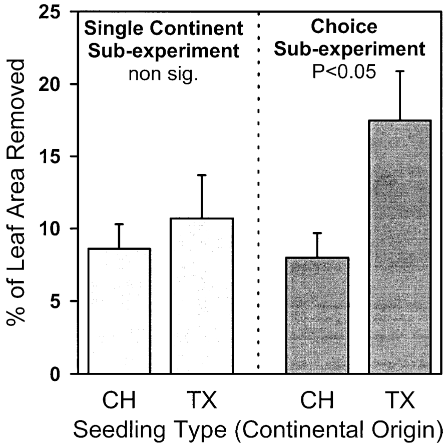

Fig. 2 Dependence of percent of *Sapium* leaf area removed in the laboratory experiment on continental origin within each sub-experiment. Means +1 SE. See Table 1 for statistics

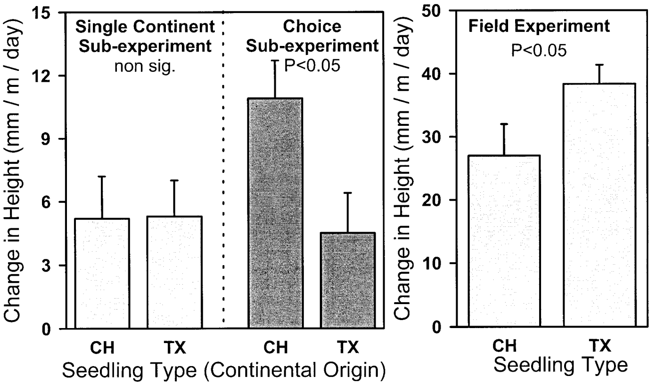

Fig. 3 (*left*) Dependence of height growth rate of *Sapium* seedlings in the laboratory experiment on continental origin within each sub-experiment. Means+1 SE. See Table 2 for statistics (*right*) Dependence of height growth rate of *Sapium* seedlings on continental origin in the field experiment. Means+1 SE. See Table 3 for statistics

sub-experiment (CH-TX 6.5 ± 1.8 mg/g perday, CH-CH 6.6±1.3, TX-TX 8.2±2.6). There was no effect of the province a Chinese seedling came from on grasshopper growth ($F_{3,\ 40}$=1.0, P=0.42). During the course of the experiment, 40 grasshoppers gained weight, 6 lost weight (3× CH-TX, 2× CH-CH, TX-TX) and 2 died or escaped.

The mass of *Sapium* foliage consumed by grasshoppers was independent of sub-experiment ($F_{1,\ 40}$=0.3, P=0.62), continent ($F_{1,\ 40}$=0.1, P=0.90) and Chinese province ($F_{3,\ 40}$=1.0, P=0.42). The amount of *Sapium* foliage consumed was 23.5±5.0 mg in the choice experiment (9.0 mg CH, 14.5 mg TX), 19.5±5.7 mg in CH-CH pots, and 20.7±7.2 mg in TX-TX pots. Grasshopper growth rates and the amount of foliage consumed were significantly positively correlated (r=+0.33, z=2.3, P<0.05).

Grass mass remaining in a pot at the end of experiment was independent of sub-experiment ($F_{1,\ 42}$=0.5, P=0.51), continent ($F_{1,\ 42}$=2.3 P=0.13) and Chinese province ($F_{3,\ 42}$=0.6, P=0.62) in a sequential ANOVA. Grasshopper growth rate and the mass of grass in pots were independent (z=–0.27, P=0.78).

In the single continent sub-experiment, percent of leaf area removed by grasshoppers was independent of continent and Chinese province (Table 1, Fig. 2). In the choice sub-experiment, grasshoppers removed a significantly greater percentage of Texas seedling leaves compared to China seedling leaves (Table 1, Fig. 2). There was no effect of Chinese province on percent of leaves removed either in the unpaired test with provinces in separate pots or the paired test with each kind in the same pot.

In the single continent sub-experiment, there was no effect of continental origin or Chinese province on height growth of *Sapium* seedlings (Table 2, Fig. 3). China seedlings grew significantly faster than Texas seedlings in the choice sub-experiment but there was no effect of Chinese province (Table 2, Fig. 3). In the entire experiment, *Sapium* seedlings grew slower as the percent of leaf area removed increased [regression: growth (mm/m per day)=9.2–0.17 × (% leaf area removed), $F_{1,\ 90}$=4.5, P<0.05].

In the field experiment, *Sapium* seedlings from China grew significantly slower than those from Texas (Table 3, Fig. 3). There was no difference in growth rate between seedlings from the different Chinese provinces. The

Table 1 Percentage of *Sapium* leaf area removed in the laboratory experiment

Sub-experiment	Factor	Test	*df*	*t*-value	*P*-value
Choice	Continent	paired	23	2.4	**<0.05**
	China province	unpaired	22	1.4	0.17
Single continent	Continent	unpaired	46	0.6	0.58
	China province	paired	4	1.0	0.37
		unpaired	10	0.5	0.61

Table 2 *Sapium* height growth rate in the laboratory experiment

Sub-experiment	Factor	*t*-Test	*df*	*t*-value	*P-value*
Choice	Continent	Paired	23	2.5	**<0.05**
	China province	Unpaired	22	0.6	0.58
Single continent	Continent	Unpaired	46	0.4	0.97
	China Province	Paired	5	1.0	0.34
		Unpaired	10	1.1	0.30

Table 3 *Sapium* height growth rate in the field experiment

Factor	*df*	Type I SS	*F*-value	*P*-value
Continent	1	379,910	5.8	**<0.05**
Province	1	31,354	0.5	0.49
Model	2	41,126	3.1	**<0.05**
Error	87	5,572,957		

average percent of leaf area removed by chewing insects was extremely low (CH=0.14%, TX=0.35%) and independent of continental origin ($F_{1,\ 90}$=0.6, *P*=0.43) and Chinese province ($F_{1,\ 90}$=1.9, *P*=0.17).

Discussion

Sapium is a suitable food source

Even though native herbivores rarely feed on *Sapium sebiferum* foliage in its introduced range (Bruce et al. 1997; Siemann and Rogers 2001), *M. angustipennis* grasshoppers readily consumed it in the laboratory experiment (Fig. 2). Since grasshopper growth rates were positively correlated with the amount of *Sapium* foliage removed and their survival rates were high even 10 days after foliage was consumed, there appears to be little, if any, toxic effect of consuming *Sapium* foliage. Indeed, it is plausible that *Sapium* foliage is an abundant, suitable food source for *M. angustipennis* or other North American insect herbivores that they nonetheless avoid consuming. A preference of generalist herbivore species for native plant species may be more related to the native or alien status of plants per se than to the nutritional quality or toxicity of the plants (Strong et al.1977; Yela and Lawton 1997). Such a preference of native generalist herbivores, along with a lack of specialist herbivores in the introduced range, is widely believed to be responsible for the success of many invasive plants (Elton 1958; Mack et al. 2000; Maron and Vila 2001; Keane and Crawley 2002; Shea and Chesson 2002).

Invasive *Sapium* genotypes were preferred to native ones

The survival and growth of grasshoppers that consumed Chinese *Sapium* foliage in the laboratory experiment (Fig. 2) showed that *Sapium* was a nutritionally suitable food source, at least for *M. angustipennis* grasshoppers, at the time when it was introduced to North America. However, grasshopper preferences for the foliage of Texas genotypes in the choice sub-experiment (Table 1, Fig. 2), where differences in preference would be manifest more strongly, indicates that invasive *Sapium* genotypes were more palatable and/or less defended than native *Sapium* genotypes (Blossey and Nötzold 1995; Daehler and Strong 1997). Although Asian *Sapium* trees have higher foliar tannin concentrations than Texas trees (Siemann and Rogers 2001), we have not found any foliar tannins in seedlings, such as used here, in other studies (Rogers and Siemann, unpublished data). Still, *Sapium* has been shown to have a variety of secondary compounds which may have a defensive function or affect palatability including coumarins (Yang and Kinghorn 1985), glycosides (Hsu et al. 1994), diterpene-esters (Ohigashi et al. 1983), and triterpenoid acids (Pradhan et al. 1984). It is possible that changes in some of these compounds were responsible for the difference in feeding rates when grasshoppers were able to choose among seedlings from the two continents.

Small differences in preference may influence *Sapium* success

Although differences in preference were modest, grasshoppers were able to influence the relative growth of *Sapium* genotypes in the choice experiment (Table 2, Fig. 3). Genotypes grew at comparable rates in the single-continent laboratory experiment in which damage rates were similar for native and invasive genotypes whereas native Chinese genotypes grew faster in the choice experiment in which damage rates were higher on invasive Texas genotypes (Tables 1, 2, Figs. 2, 3). Differences in growth are unlikely to have been the result of non-genetic differences in seed quality (i.e. maternal effects, Willis et al. 2000), which are strongest in the earliest stages of growth, because seedling height did not depend on genotype at the start of the laboratory ($F_{2,\ 93}$=2.0, *P*=0.13) or field experiments ($F_{2,\ 87}$=1.0, *P*=0.39). Even a fine difference in preference may be ecologically significant if herbivores frequently have the opportunity to choose among individual plants (O'Reilly-Wapstra et al. 2002) or plant parts (Pavia et al. 2002) that differ in their defense. The reversal of relative growth rates of genotypes in the choice experiment, compared to the field experiment and equivalence in the single-continent laboratory experiment (Tables 2, 3, Fig. 3), may mean that native herbivores have the potential to reduce the intensity of *Sapium* invasion by selecting against fast-growing, poorly-defended invasive *Sapium* individuals. This more typical relationship between defense and herbivore attack (Coley et al. 1985) would eliminate the combination of low damage and low defense that contributes to invasive plant success in the EICA hypothesis. However, because we did not grow Texas and China *Sapium* seedlings in competition in pots without grasshoppers, we do not know for certain that Texas seedlings would have outcompeted the China seedlings as they did in the field with almost no herbivory.

In the field experiment, Texas *Sapium* seedlings grew faster than seedlings from either Chinese province (Table 3, Fig. 3). The consistency of this result and a 14-year common garden experiment with different sets of seeds from Asia and North America (Siemann and Rogers 2001) is evidence that North American *Sapium* genotypes may be faster growing and less-defended, in general, than

Asian *Sapium* genotypes. So long as herbivory levels are comparable on well-defended and poorly-defended genotypes, plants that have lower defense should have higher fitness (Simms and Rausher 1987; Maschinski and Whitham 1989). It is possible that differences between the field and laboratory conditions, such as light levels, are responsible for the absolute differences in growth rates in the field and laboratory experiments.

Herbivores and novel food plants

Insect herbivores consumed very little foliage of any genotypes of *Sapium* in the common garden field experiment. Since *M. angustipennis* grasshoppers, abundant in the field, fed on *Sapium* foliage in laboratory experiments (Table 1, Fig. 2) and survived and gained weight by doing so, biochemical barriers to their consumption of *Sapium* foliage are weak or do not exist. Rather, *Sapium* may be a suitable food choice that is avoided because there is strong selection against host range expansion when new host plants may be toxic (Chew and Courtney 1991), temporally or spatially uncommon (Chew and Courtney 1991; Beccaloni and Symons 2000) or of limited use due to the influence of herbivore natural enemies (Camara 1997). If the process of host range expansion requires biochemical or nutritional acceptability as a prerequisite to behavioral adaptation, any costs of experimentation in the presence of other acceptable food sources may greatly delay the inclusion of new food items. At least for broadly planted crops and trees, this delay appears to be of the order of a century (Strong 1974; Strong et al. 1977).

Because there is no parental care in Melanopline grasshoppers, and females lay their eggs in suitable areas that are not associated with particular host plants (Huntly and Inouye 1988), there is likely little role for maternal effects (Fox et al. 1997; Fox and Savalli 2000; Solarz and Newman 2001) in the feeding preferences of *Melanoplus* grasshoppers. However, the experience of early instar grasshopper nymphs may have a strong effect on host selection by adults in other species of Acridid grasshoppers. Indeed, some grasshoppers have a strong affinity for host plants they feed on as nymphs that cannot easily be overcome by conditioning later in life (Traxler and Joern 1999). In any case, since there is little or no herbivory on *Sapium* in the field, it is unlikely that the preference for local varieties (Table 1, Fig. 2) reflects consumption of *Sapium* by grasshoppers in early life stages.

Conclusions

The lower herbivore resistance of invasive genotypes of *Sapium* (Table 1, Fig. 2) suggests their invasive success in North America may be due in part to an evolutionary reallocation of resources from defenses to growth (Siemann and Rogers 2001; Rogers and Siemann 2003). In the EICA scenario (Blossey and Nötzold 1995), such a reallocation is a consequence of high costs of defenses when herbivory is low and independent of defenses. However, the advantage invasive genotypes may obtain from low defense costs is in addition to the advantage both native and invasive genotypes receive from low herbivore damage in Texas. The combination of low herbivory and low defenses that native plants cannot achieve may give *Sapium* and other invasive species a competitive advantage and may explain their invasive success.

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