

Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies

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Abstract. 1. Introduced plants generally have lower generalist herbivore loads than native plants. Herbivores may be avoiding a potentially edible food source (Behavioural Constraint Hypothesis) or defences of introduced plants may be unusually toxic (Novel Defence Hypothesis).

2. To examine these hypotheses, acridid grasshoppers (*Melanoplus angustipennis* and *Orphulella pelidna*) were enclosed in a Texas grassland. Each enclosure contained native prairie vegetation and a seedling of either introduced *Sapium sebiferum* (Chinese tallow tree) or native *Celtis laevigata* (hackberry). *Sapium* invades many ecosystems in the south-east U.S.A. *Celtis* seedlings also establish in these ecosystems.

3. Although grasshoppers usually feed sparingly on *Sapium*, in field enclosures they fed heavily on this introduced tree species, supporting a role for behavioural avoidance. In laboratory feeding trials, *M. angustipennis* grasshoppers preferred *Sapium* foliage over the foliage of three native tree species. In a greenhouse experiment, *M. angustipennis* individuals fed more on *Sapium* in prairie mesocosms if they were conditioned on *Sapium*.

4. In another field experiment with single seedlings in enclosures, grasshoppers consumed similar amounts of *Sapium* from its introduced (Texas, U.S.A.) and native (China) ranges, suggesting that *Sapium* may have been a suitable host plant since it was introduced. Behavioural avoidance by generalist herbivores may contribute to *Sapium*'s low herbivore load in its introduced range.

Key words. Behavioural constraint, enemies hypothesis, generalist herbivore, grasshopper, invasive species, *Sapium sebiferum*.

Introduction

Biological invasions present an unique opportunity for ecologists to study the interactions between plants and herbivores (Elton, 1958; Lodge, 1993; Williamson, 1996; Mack *et al.*, 2000). Herbivores affect plant communities by feeding preferentially on some species or functional groups (Ritchie & Olff, 1999). Recently introduced plants are generally found to have lower herbivore loads in their introduced ranges

than in their native range, as well as lower loads compared with native plants in their new range (e.g. Southwood *et al.*, 1982; Strong *et al.*, 1984; Yela & Lawton, 1997; Keane & Crawley, 2002). This may explain why introduced plants often competitively exclude native plants (Elton, 1958; Williamson, 1996; Keane & Crawley, 2002).

Introduced plants may have low herbivore loads for at least two reasons: they are usually introduced with few or none of the specialist herbivores from their native range and generalist herbivores in their new range cannot or prefer not to feed on them (e.g. Elton, 1958; Lodge, 1993; Tilman, 1999; Keane & Crawley, 2002). However, introduced plants typically support diverse insect communities in their new range within 300 years (Strong, 1974; Strong *et al.*, 1977).

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Since specialist herbivores generally have a suite of physiological and behavioural adaptations to their host species, it is not surprising that native specialists generally do not feed on newly introduced species (Leather, 1986; Bernays & Chapman, 1994). Generalists have less restrictive requirements for host plants, so it is unclear why some native generalists do not immediately utilise introduced plants. Two alternative hypotheses may explain this delay. Introduced plants may possess novel biochemical defences to which native generalists are not adapted (Novel Defence Hypothesis). In this case, herbivores must evolve new physiological or biochemical adaptations before they can utilise the new plant, creating a time lag. Alternatively, native generalists may be able to feed on the introduced plant but lack the behavioural adaptations necessary to recognise it as a suitable food source under natural conditions (Behavioural Constraint Hypothesis). Insects may avoid plants that they do not recognise to reduce the risk of feeding on a toxic plant (Feeny, 1975; Abrahamson & Weis, 1997). Insects may also ignore novel plants due to neurological constraints that only allow them to recognise specific chemical cues (Bernays & Chapman, 1994; Bernays, 2001). Therefore, native insects may not utilise novel plants, even though the new plant may be palatable. If these behaviours are fixed, then evolutionary changes are required before the native generalists begin to feed on introduced plants, similar to the novel defence situation; however, feeding behaviour in generalists is often plastic (Bernays & Chapman, 1994). If this is the case, then changes in the context in which native generalists come in contact with introduced plants may be sufficient for the herbivores to overcome these constraints and begin to utilise the novel species.

Comparison of native and introduced species

The interaction of two grasshopper species with the introduced Chinese tallow tree [*Sapium sebiferum* (L.) Roxb., Euphorbiaceae] was studied through laboratory and field experiments to explore these alternative explanations. Under natural conditions, *Sapium* experiences extremely low levels of generalist herbivory both in absolute terms and relative to native tree seedlings (Siemann & Rogers, 2003a). Grasshopper interactions with seedlings of native hackberry, *Celtis laevigata* Willd. (Ulmaceae) and seedlings of *Sapium* from naturalised populations in Texas were compared when grasshoppers were confined with seedlings and native grassland vegetation. *Sapium* is potentially vulnerable to regulation by herbivores in the seedling stage, when it faces strong competition from native grasses and forbs. Therefore, all field experiments were performed on seedlings rather than mature plants. Grasshopper feeding preferences were also determined for mature *Sapium* versus mature leaves of three native tree species in a laboratory experiment. The Novel Defence Hypothesis predicts that grasshoppers will feed more on native plants than on *Sapium* under all conditions. The Behavioural Constraint Hypothesis makes different

predictions, depending on the nature of the behaviour. If feeding behaviour is fixed for an individual grasshopper, then the predictions of the Novel Defence and Behavioural Constraint hypotheses are identical; however, if feeding behaviour is plastic, then the Behavioural Constraint Hypothesis predicts that grasshoppers may utilise *Sapium* to a greater extent than native plants when confined, in contrast to the situation observed under natural conditions.

An experiment was performed in which grasshoppers were conditioned with either *Sapium* or *Celtis* then released into a large prairie mesocosm containing a *Sapium* seedling. Insects, including grasshoppers, have been shown to alter their feeding behaviour due to experience (Bernays & Chapman, 1994). Some insects, especially lepidopterans, are known to induce a preference for plants experienced previously (Deboer & Hanson, 1984). If the Behavioural Constraint Hypothesis explains avoidance of *Sapium* by native herbivores, grasshoppers may learn to prefer *Sapium* over native plants. Similarly, if *Sapium* contains compounds that deter feeding but do not affect performance, grasshoppers may habituate to the chemical and be more likely to feed on *Sapium* in the mesocosm (Jermy *et al.*, 1982; Bernays & Chapman, 1994). Alternatively, if the Novel Defence Hypothesis explains avoidance of *Sapium* by native herbivores, grasshoppers may sensitise to the toxin and avoid *Sapium* (Lee & Bernays, 1990; Bernays & Chapman, 1994).

Comparison of native (China) and introduced (Texas, U.S.A.) varieties of Sapium

The Evolution of Increased Competitive Ability hypothesis proposes that introduced plant species evolve higher allocation of resources to growth and reproduction and lower allocation to defence (Blossey & Nötzold, 1995). *Sapium* varieties from North America maintain lower levels of foliar tannins, grow faster, and set more seed than varieties from Asia in Texas common gardens as predicted by this hypothesis (Siemann & Rogers, 2001). Native varieties of *Sapium* also have higher herbivore resistance than invasive varieties in lab microcosms with Texas grasshoppers (Siemann & Rogers, 2003b) and experience lower damage from Asian herbivores in common gardens in Hawaii (Siemann & Rogers, 2003c).

If *Sapium* has reduced its defences since introduction, then it may have only recently become palatable to native generalist herbivores. A second field experiment was performed using *Sapium* seedlings derived from its native (China) and introduced (Texas, U.S.A.) ranges. Chinese seedlings were used to approximate the situation when *Sapium* was introduced. If *Sapium* has only recently become an acceptable food source, grasshoppers will feed on the Texan seedlings to a greater extent. If grasshoppers feed on both types of seedlings similarly, this would be evidence that *Sapium* has always been a suitable food source.

Materials and methods

Study site

Field experiments were conducted in a coastal prairie at the University of Houston Coastal Center, a 374-ha research area located ≈ 50 km south-east of Houston in LaMarque, Texas, U.S.A. This area is invaded aggressively by *Sapium* so the prairies are mowed annually to suppress woody plant invasion (Bruce *et al.*, 1997). Mowed areas are dominated by native graminoids (82% of biomass), with *Schizachyrium scoparium* Gould the dominant species (Harcombe *et al.*, 1993). Forbs and woody plants comprise the rest of the plant cover.

Focal species

Sapium sebiferum is a major invader of ecosystems of the south-eastern U.S.A. (Bruce *et al.*, 1997). It was introduced intentionally in the late 18th century to Georgia and has been planted commonly as a biomass crop, oil crop, nectar crop, and ornamental (Bruce *et al.*, 1997). *Sapium* was introduced to Texas 100 years ago where it readily invades native coastal prairies and displaces native flora (Bruce *et al.*, 1997).

Sapium is believed to benefit from lower herbivore loads in its introduced range (e.g. Harcombe *et al.*, 1993; Bruce *et al.*, 1997). A variety of generalist and specialist insects feeds on *Sapium* in its native range (Zhang & Lin, 1994); however, it faces low herbivore levels in its introduced range. In Texas coastal prairies, naturally established *Sapium* seedlings have lower levels of herbivore damage than on native tree seedlings (Rogers & Siemann, 2002). Similarly, field studies of experimentally planted *Sapium* and native trees reveal less leaf damage on *Sapium* seedlings (Siemann & Rogers, 2003a).

Celtis was included in these studies because grasshoppers probably interact differently with woody *Sapium* than with native prairie forbs and grasses in part due to gross morphological and phenological differences unrelated to *Sapium*'s introduced status. Ideally, the two species would be congeners, but no other species of *Sapium* occur in the area. *Celtis* is the most ecologically similar native tree

species that occurred commonly at the site. Both *Celtis* and *Sapium* are insect pollinated, bird dispersed, tend to grow in wetter sites, and have the potential to grow rapidly (Bruce *et al.*, 1997; Siemann & Rogers, 2003a). Under natural conditions, *Celtis* suffers substantially higher levels of herbivory than *Sapium* (Siemann & Rogers, 2003a). Using *Celtis* made it possible to more clearly determine how interactions of herbivores with introduced versus native species differ.

Grasshoppers are a good model organism to study generalist herbivory in prairies because they are among the most abundant and important herbivore groups in prairie systems and have broad feeding habits (Risser *et al.*, 1981). Moreover, grasshoppers are amenable to herbivore enclosure studies because they are large enough to allow handling and identification in the field (Belovsky, 1986; Ritchie & Tilman, 1992; Schmitz, 1993).

Acridid grasshoppers are abundant and important herbivores in prairies (Risser *et al.*, 1981). Acridid grasshoppers were censused during the first week of June 2000 by repeated sweep net sampling in a floristically similar field adjacent to the study site. The two most abundant species were used in the experiment (Table 1). *Orphullela pelidna* are generalist graminoid feeders (Evans, 1992) while *Melanoplus angustipennis* are generalist graminoid and forb feeders (Ueckert & Hansen, 1971). Most individuals in both populations were in the adult stage at the time of collection. Species identifications were confirmed with the assistance of the entomological collections at Texas A & M University (College Station, Texas).

Interspecific herbivore enclosure experiment

Seeds of *Sapium* and *Celtis* were collected at the University of Houston Coastal Center during October and November 1999, and germinated in an unheated greenhouse in March 2000. Each germinated seed was transferred to a 100-ml Conetainer (Stuewe & Sons, Inc. Corvallis, Oregon) filled with a mixture of commercially available topsoil (2/3) and organic humus and peat (1/3). Seedlings were moved outside under a 50% shade cloth to harden off after developing primary leaves. All seedlings were watered daily. This protocol was used for all studies.

Table 1. Species richness and abundances for the acridid community at the University of Houston Coastal Center. All specimens were collected on 6 or 7 June 2000 from a roughly 25-m² area.

Species	Subfamily	Abundance	Per cent
<i>Amblytropidia mysteca</i> (Saussure)	Gomphocerinae	2	0.5
<i>Chortophaga viridifasciata</i> (DeGeer)	Oedipodinae	6	1.5
<i>Hesperotettix speciosus</i> (Scudder)	Melanoplinae	1	0.3
<i>Melanoplus angustipennis</i> (Dodge)	Melanoplinae	102	25.8
<i>Melanoplus femurrubrum</i> (DeGeer)	Melanoplinae	22	5.6
<i>Melanoplus plebejus</i> (Stal)	Melanoplinae	2	0.5
<i>Orphullela pelidna</i> (Burmeister)	Gomphocerinae	257	64.9
<i>Paroxya atlantica</i> (Scudder)	Melanoplinae	1	0.3
<i>Trachyrhachys kiowa</i> (Thomas)	Oedipodinae	3	0.8

The experimental field was mowed 2 weeks prior to transplanting the tree seedlings. A grid of 48 1-m² plots was established and grasshopper density and tree seedling species treatments were assigned randomly to each plot in a complete factorial design. A *Sapium* or *Celtis* seedling was transplanted into the centre of each plot on 15 May 2000. The plots were watered periodically.

Grasshopper enclosures were placed over each seedling and the adjacent prairie vegetation 2 weeks after planting (*sensu* Belovsky, 1986; Ritchie & Tilman, 1992; Schmitz, 1993). The cylindrical enclosures were 1.22 m tall and 0.58 m in diameter (area 0.26 m²). They were constructed of 0.16-mm mesh aluminium window screen joined to a 10-cm tall strip of aluminium sheeting. The aluminium sheeting was buried 5 cm beneath the soil surface and anchored with steel rods to prevent grasshoppers from escaping. Personal communication with O. Schmitz ensured that the cages and methods matched those of previous studies (Schmitz, 1993, 1998).

Four weeks after seedlings were planted, adult grasshoppers were collected at The University of Houston Coastal Center. They were stored overnight in indoor terrariums then placed in the enclosures. High-density enclosures (H) received eight grasshoppers (four *M. angustipennis*: two females and two males; four *O. pelidna*: two females and two males); low-density enclosures (L) received four grasshoppers (same ratios); control enclosures (N) were left empty. After grasshoppers were added, the tops of all the enclosures were folded over and secured with binder clips. The lower density was chosen to approximate the background density of grasshoppers at this site at that time of the year. This was estimated through sweep net sampling in an adjacent field 2 weeks before the start of the experiment (Table 1). The high-density treatment was used to represent the natural patchiness in grasshopper abundance, and was well within the range of grasshopper densities found in the census. Five days after the original stocking, additional grasshoppers of the appropriate species and sex were caught and added to enclosures to replace any individuals that had died due to handling or transport stress.

The experiment ran for 35 days after restocking. This time period is similar to other studies (e.g. Ritchie & Tilman, 1992; Schmitz, 1993; Schmitz, 1994). Grasshopper densities were censused visually 16 days after restocking by blowing the enclosures gently with a hand air pump. All living grasshoppers remaining at the end of the experiment were caught and frozen. The enclosures were removed, and the height, basal stem diameter, and number of leaves were measured for each *Celtis* and *Sapium* seedling. The per cent leaf area removed by herbivores was visually estimated by a single observer (R. A. Lankau). Previous experiments have quantified leaf area removal with a computer imaging program, and the results were consistent with visual estimates. Seedlings were clipped at ground level, and the stems and leaves were bagged separately. All remaining above-ground vegetation was harvested and sorted to functional group (graminoid, forb, and woody). Plant mass was dried at 60 °C for 48 h then weighed.

Laboratory preference experiment

A laboratory feeding trial was conducted with *M. angustipennis* to examine the preference of grasshoppers for the foliage of *Sapium* versus native trees. In late summer 2000, grasshoppers and leaves from four species of trees [*Sapium*, *Celtis*, *Liquidambar styraciflua* L. (Sweetgum), and *Platanus occidentalis* L. (Sycamore)] were collected at The University of Houston Coastal Center. All except *Sapium* are native to the region. One grasshopper was placed in each of six 5.6-litre plastic containers along with leaves from each species. Each container received five *Sapium* leaves, five *Celtis* leaves, one *Liquidambar* leaf, and one *Platanus* leaf. The number of leaves differed to help control for differences in leaf size among species. All leaves had their petioles in water and remained hydrated throughout the experiment. Containers were placed in a growth chamber and kept at 25 °C with 12 h of light daily. After 3 days, the per cent of total leaf area removed was visually estimated, and the remaining foliage was dried and weighed to estimate the amount of biomass consumed.

Greenhouse conditioning experiment

In summer 2002, a greenhouse experiment was performed to determine whether *M. angustipennis* grasshoppers could be conditioned to feed on *Sapium*. The experiment consisted of a conditioning phase and a test phase. During the conditioning phase, adult grasshoppers were confined in small screen cages placed over a 9-litre treepot containing gulf annual ryegrass *Lolium multiflorum* Lam. (Pennington Seed Inc., Lebanon, Oregon) and a seedling of either *Sapium* or *Celtis* (four replicates each). After 1 week, chewing damage on each seedling was measured and each grasshopper was transferred into a separate prairie mesocosm. Mesocosms were topsoil filled plastic bins (area 1 m²) covered by mosquito netting (150 × 81 × 198 cm), and seeded with annual ryegrass and a mixture of native Texas coastal prairie forbs 1 month prior to the start of the experiment (Earthseeds.com, Santa Fe, New Mexico). One *Sapium* seedling was placed into the centre of each of the eight mesocosms. Grasshoppers remained in mesocosms for 2 weeks (test phase). The experiment was run in three consecutive rounds, with the first round using all male grasshoppers and the last two using all females. Adult grasshoppers were collected immediately prior to each round from The University of Houston Coastal Center. Chewing damage was recorded on each seedling every 2 days, and at the end of the experiment, leaves were scanned and analysed using a computer program (NIH Image, <http://rsb.info.nih.gov/nih-image/>) for a more precise measurement of total leaf area removed. Grasshoppers were weighed immediately before and after the experiment to determine growth rates.

Intraspecific herbivore enclosure experiment

In summer 2001, a field experiment was performed using *Sapium* seedlings grown from seeds collected at The University of Houston Coastal Center and seeds from Guangdong, China. Field methods were identical to those in the first field experiment. Three grasshopper treatments were used (no cage controls, empty cages, and cages with four *M. angustipennis*). Each treatment combination was replicated 12 times for a total of 72 plots. Seedlings were planted on 22 May 2001; cages were added after 2 weeks and grasshoppers after 4 weeks, as in the previous experiment.

Naturally occurring seedlings

Since the seedlings in all experiments were germinated in a greenhouse, they may have differed in leaf quality from naturally occurring seedlings that have experienced natural levels of competition and herbivory. To control for this, six naturally occurring *Sapium* seedlings were chosen at the site and enclosed in small screen cages. Two *M. angustipennis* grasshoppers were added to each cage and left for 1 week. Chewing damage was then estimated as in the previous experiments. These results were compared with the previous experiments to determine if grasshoppers responded differently to greenhouse grown versus naturally occurring seedlings.

Analyses

Ordinary least-squares linear regressions were used to determine how grasshopper density in the interspecific herbivore enclosure experiment affected chewing damage on *Sapium* seedlings, chewing damage on *Celtis* seedlings, final *Sapium* seedling mass, final *Celtis* seedling mass, above-ground community biomass (total and by functional group), and how the amount of *Sapium* consumed in the conditioning experiment affected grasshopper growth rate. Chewing damage was arcsine (square-root) transformed and seedling biomass was square-root transformed for all experiments to meet the assumptions of the analyses. A one-way ANOVA was used to compare the amounts of each plant species consumed in the laboratory preference experiment, and Fisher's LSD was used to compare means among species since no *a priori* predictions were made for the treatments. A two-way ANOVA was used for the greenhouse conditioning experiment to determine the effects of conditioning species (*Sapium* or *Celtis*), experiment round, and their interaction on *Sapium* consumed during the test phase and growth rate of the grasshoppers. Orthogonal contrasts were used to compare differences among male and female grasshoppers, and to test for an interaction of sex and conditioning treatment for both variables. A two-way ANOVA was also used for the intraspecific herbivore enclosure experiment to determine how chewing damage on *Sapium* seedlings and final *Sapium* biomass depended on seedling variety and grasshopper treatments, and orthogonal

contrasts were then used to determine if seedlings in stocked cages differed significantly from those in empty cages or in the open prairie, and if this effect depended on seedling variety. A *t*-test was used to determine if grasshopper growth rates were significantly different from zero in the conditioning experiment. All analyses were performed using STATVIEW 5.0 or SAS 8.0 (SAS Institute, Cary, North Carolina).

Results*Interspecific herbivore enclosure experiment*

Grasshopper density affected *Sapium* and *Celtis* seedlings differently. Leaf damage increased with grasshopper density for both seedling species in linear regressions; however, *Sapium* damage increased more strongly as grasshopper density increased (Fig. 1). *Sapium* biomass decreased significantly with grasshopper density but *Celtis* seedling biomass was unaffected (Fig. 2). Grasshopper density did not affect total above-ground community biomass ($P = \text{NS}$) or biomass of any functional group (graminoid, forb, woody, all $P = \text{NS}$).

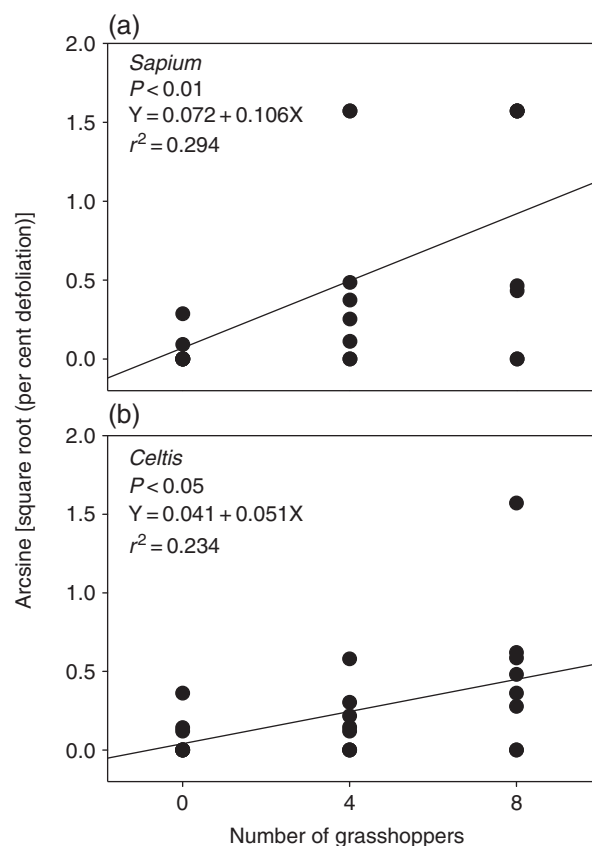


Fig. 1. Interspecific herbivore enclosure experiment. Dependence of per cent leaf removal (arcsine square-root transformed) on initial grasshopper density for (a) *Sapium* and (b) *Celtis* seedlings. Lines and equations are from ordinary least-squares regressions.

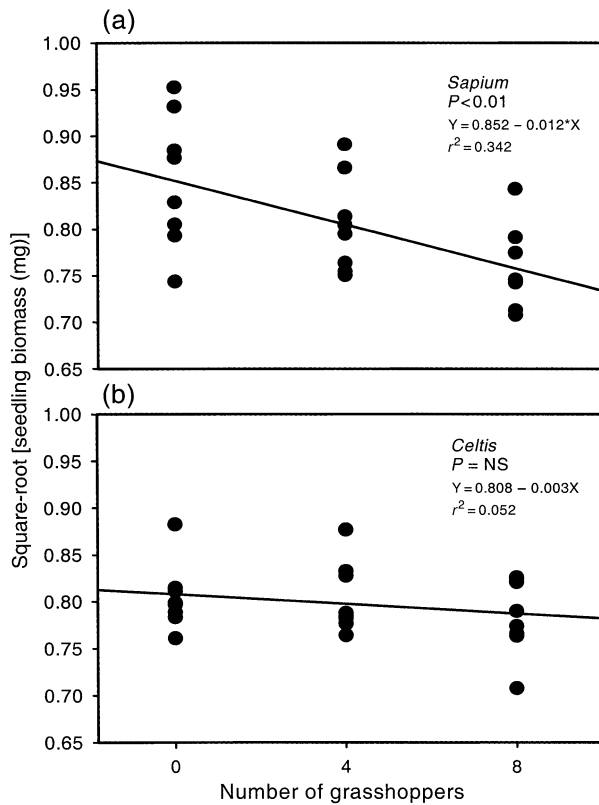


Fig. 2. Interspecific herbivore enclosure experiment. Dependence of final seedling biomass (square-root transformed) on initial grasshopper density for (a) *Sapium* and (b) *Celtis* seedlings. Lines and equations are from ordinary least-squares regressions.

Laboratory preference experiment

Grasshopper consumption differed significantly among the four species ($F_{3,15} = 21.3$, $P < 0.001$). Means comparisons showed that grasshoppers consumed significantly more *Sapium* than other species, and *Celtis* was preferred over the two other native species (Fig. 3). The six containers did not differ in the percentage of leaf area consumed ($F_{5,15} = 0.56$, $P = \text{NS}$).

Greenhouse conditioning experiment

Grasshoppers conditioned on *Sapium* consumed more *Sapium* in mesocosms than those conditioned on *Celtis* ($F_{1,12} = 4.923$, $P < 0.05$; Fig. 4). Chewing damage was independent of round ($F_{2,12} = 1.514$, $P = \text{NS}$) and interaction of round and conditioning treatment ($F_{2,12} = 0.425$, $P = \text{NS}$). Male and female grasshoppers did not differ in their consumption patterns (male round versus average of female rounds, $F_{1,12} = 2.62$, $P = \text{NS}$), and this effect did not differ between conditioning treatments (interaction of sex $\times$ treatment, $F_{1,12} = 0.3$, $P = \text{NS}$).

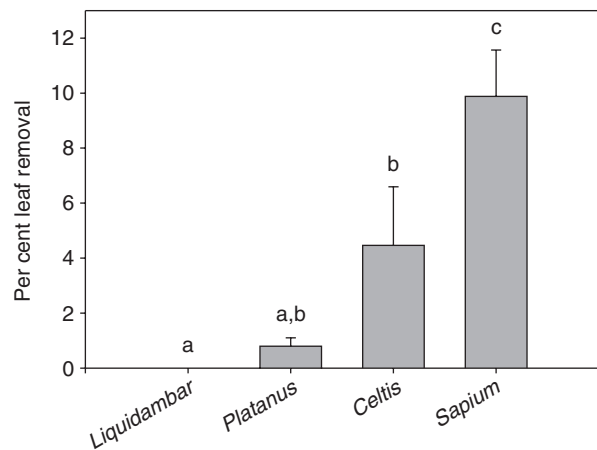


Fig. 3. Leaf consumption by species in laboratory preference test. Bars are back-transformed means $\pm$ SE. Means with the same letter are statistically indistinguishable at $P < 0.05$. Significance levels were determined by analysis of arcsine square-root transformed data.

Grasshopper growth rate [(final weight – initial weight)/initial weight] did not differ among treatments ($F_{1,17} = 0.659$, $P = \text{NS}$), rounds ($F_{2,17} = 1.676$, $P = \text{NS}$), or their interaction ($F_{2,17} = 1.812$, $P = \text{NS}$) in the combined ANOVA. Contrasts showed no significant differences in growth rates of males and females ($F_{1,12} = 0.02$, $P = \text{NS}$), and no interaction between sex and conditioning treatment ($F_{1,12} = 1.14$, $P = \text{NS}$). The total amount of *Sapium* consumed (sum of conditioning and testing phases) did not affect grasshopper growth rate ($R^2 = 0.031$, $P = \text{NS}$). Grasshoppers maintained an overall positive growth rate throughout the 3-week experiment (mean = 0.1, $t_{11} = 1.371$, $P < 0.01$), and all grasshoppers survived the entire experiment.

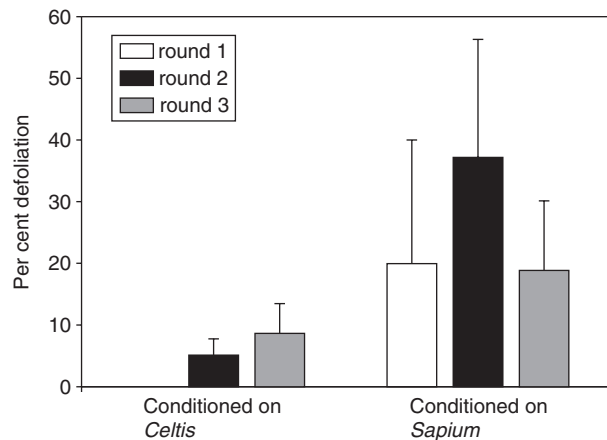


Fig. 4. Greenhouse conditioning experiment. Dependence of per cent leaf removal on *Sapium* seedlings in prairie mesocosms on conditioning treatment and experimental round. Bars are back-transformed means $\pm$ SE. Means with the same letter are statistically indistinguishable at $P < 0.05$. Significance levels were determined by analysis of arcsine square-root transformed data.

Intraspecific herbivore enclosure experiment

Grasshopper effects on *Sapium* seedlings from Texas or China did not differ. Chewing damage depended on grasshopper treatment ($F_{2,64}=21.2$, $P<0.001$; Fig. 5a), but not *Sapium* variety ($F_{1,64}=0.03$, $P=NS$; Fig. 5a) or their interaction ($F_{2,64}=0.09$, $P=NS$). Contrasts showed that damage was higher on seedlings in the stocked cages compared with seedlings in the empty cages or open prairie ($F_{1,64}=42.21$, $P<0.001$), but this effect did not depend on the seedling variety ($F_{1,64}=0.14$, $P=NS$ for interaction). Similarly, seedling biomass was reduced by grasshoppers ($F_{2,64}=17.08$, $P<0.0001$; Fig. 5b) but independent of seedling variety ($F_{1,64}=1.55$, $P=NS$; Fig. 5b) and their interaction ($F_{2,64}=0.71$, $P=NS$). Biomass was reduced in stocked cages compared with seedlings in empty cages or open prairie (contrast, $F_{1,64}=33.88$, $P<0.001$), but this effect did not differ between the varieties (contrast, $F_{1,64}=1.14$, $P=NS$).

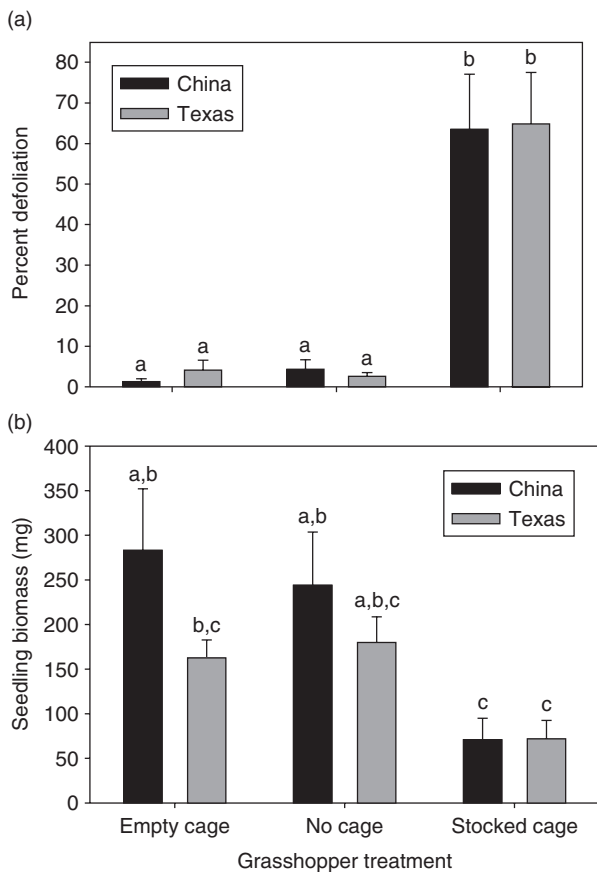


Fig. 5. Intraspecific herbivore enclosure experiment. Dependence of (a) per cent leaf removal and (b) final seedling biomass on grasshopper treatment and seedling variety. Bars are back-transformed means $\pm$ SE. Means with the same letter are statistically indistinguishable at $P<0.05$. Significance levels were determined by analysis of (a) arcsine square-root or (b) square-root transformed data.

Naturally occurring seedlings

For grasshoppers caged over naturally occurring *Sapium* seedlings, damage levels were comparable to those on caged seedlings in the previous two field experiments (mean = 40.9%, SE = 12.1%), indicating that grasshoppers responded similarly to greenhouse grown and naturally occurring *Sapium* seedlings.

Discussion

These results support the Behavioural Constraint Hypothesis. In the interspecific herbivore enclosure experiment, grasshoppers utilised *Sapium* seedlings to a greater extent than native *Celtis* seedlings (Figs 1 and 2). This was confirmed in the laboratory because *M. angustipennis* grasshoppers consumed *Sapium* leaves more than leaves from three native trees (Fig. 3). The Novel Defence Hypothesis predicted that *Sapium* would be avoided under all conditions. Only a plastic behavioural constraint would allow for *Sapium* to be avoided in open prairie conditions but preferred in confined conditions. The conditioning experiment provided further support for the Behavioural Constraint Hypothesis, because grasshoppers with experience on *Sapium* were more likely to feed on *Sapium* in prairie mesocosms and did not suffer negative physiological effects (Fig. 4). Together these results suggest that *Sapium* does not produce unusually effective physical or chemical defences to discourage a generalist herbivore. The intraspecific herbivore enclosure experiment indicated that *Sapium* has likely been a suitable food source for *M. angustipennis* since it was first introduced (Fig. 5). Despite being present in the area for a century, and being very abundant in Galveston county for at least 30 years, *Sapium* continues to experience low herbivory in part because native herbivores choose not to eat it.

Comparison of introduced and native species

The results from the interspecific herbivore enclosure experiment suggest a behavioural constraint on the use of *Sapium* by these grasshopper species (Figs 1 and 2). If grasshoppers were constrained by novel *Sapium* defences, chewing damage on *Sapium* seedlings would have been less than that on native *Celtis* seedlings, because *Celtis* has no known unusual chemical defences, is common at this site, and has been shown to suffer greater amounts of foliar chewing damage than *Sapium* in the open prairie (Van Aiken & Lohstroh, 1990; Rogers *et al.*, 2000; Siemann & Rogers, 2003a). Instead, *Sapium* suffered very high levels of damage in cages, higher than those of *Celtis* seedlings in cages or naturally established *Sapium* seedlings in nearby prairie (Fig. 1). The difference in *Sapium* damage between the open prairie (approximately 4%, Fig. 5) and in cages (approximately 50% in both experiments, Figs 1 and 5) suggests that the grasshoppers are fully capable of feeding on *Sapium*, but do not recognise it as a suitable

host plant under natural conditions. When confined, however, they seem more likely to experiment with new food sources. *Melanoplus* grasshoppers require a mixed diet of dicots and monocots (Ueckert & Hansen, 1971); however, because neither total community biomass nor the biomass of any functional group depended on grasshopper density in this experiment, it does not appear that the grasshoppers were food limited and fed on *Sapium* out of necessity when other plants were depleted. Similar results were obtained in the laboratory preference experiment, in which grasshoppers preferred *Sapium* strongly over three native tree species (Fig. 3).

The conditioning experiment provided additional support for the Behavioural Constraint Hypothesis. With experience, grasshoppers learned to prefer *Sapium* and recognised it as a favoured food source even in large prairie mesocosms with very low grasshopper densities (Fig. 4). Damage on *Sapium* seedlings in mesocosms with unconditioned grasshoppers (< 5%) was similar to that seen on naturally occurring *Sapium* seedlings in the open prairie; however, in mesocosms with *Sapium* conditioned grasshoppers, damage on the seedling (approximately 30%) was more like that in the field experiment, despite a 16-fold reduction in grasshopper density. This suggests that *Sapium* is palatable to grasshoppers, but that naive individuals do not recognise it as such. If *Sapium* had effective biochemical defences, conditioned grasshoppers would have developed an aversion to the toxic plant, and damage on seedlings in mesocosms would have been less than in controls (Lee & Bernays, 1990). This effect may explain the results of the interspecific herbivore enclosure experiment; grasshoppers were initially prompted to sample the seedling due to their confinement, and feeling no ill effect, continued to feed on the seedling throughout the experiment.

Grasshopper performance, including both growth rate and survival, was not affected negatively by *Sapium* consumption, contrary to the predictions of the Novel Defence Hypothesis. Unfortunately, practical considerations made it impossible to measure lifetime fitness for this species; however, weight gain is highly correlated with fitness for adult grasshoppers, especially ovipositing females (del Castillo *et al.*, 1999).

Several lines of reasoning suggest that it would be advantageous for a generalist insect to avoid novel plants. Insect host ranges are determined at least partly by the secondary chemicals of plants (Dethier, 1941; Ehrlich & Raven, 1964; Feeny, 1975). Herbivores are expected to feed only on plants to which they have adapted effective countermeasures. This is well documented in specialist species (Ehrlich & Raven, 1964; Feeny, 1975; Abrahamson & Weis, 1997), but generalists also have detoxification mechanisms to common chemical defences and show varying amounts of selectivity in their host choices (Bernays & Chapman, 1994). Dietary experimentation is generally selected against, as the risks of selecting a toxic plant exceed the benefits of gaining an additional food source (Feeny, 1975; Abrahamson & Weis, 1997). Restricted host ranges may also have evolved due to pressure from natural enemies and selection for behavioural efficiency (Bernays, 2001). Insects with many potential hosts are less efficient in their decisions,

and therefore suffer increased vulnerability to natural enemies. Thus insects have evolved to recognise specific chemical cues associated with suitable hosts quickly, and to ignore or avoid plants that lack these cues (Bernays & Chapman, 1994; Bernays, 2001).

In either case, the artificial environment in the cages may have altered the risks and benefits of experimentation for grasshoppers. It has been shown that the feeding behaviour of individual insects, including host choice, can be altered by environmental context (Bernays & Chapman, 1994). Grasshoppers have been shown to habituate to harmless deterrent chemicals (Jermy *et al.*, 1982), as well as sensitize to previously ignored phagostimulatory compounds (Bernays & Chapman, 1974). Either scenario could explain the results of both the field and conditioning experiments. In addition, the grasshoppers were protected from predators in these cages, so long decision times were not as costly. Generalist grasshoppers can modify their feeding behaviour based on the perceived risk of predation (Schmitz, 1998; Pitt, 1999).

Comparison of native (China) and introduced (Texas, U.S.A.) genotypes of Sapium

Introduced plants may be selected to reduce their investment to defence if they face low herbivore loads in their new range (Blossey & Nötzold, 1995; Willis *et al.*, 1999). *Sapium* individuals from its introduced range have been shown to have lower levels of foliar tannins compared with individuals from its native Asian range (Siemann & Rogers, 2001). This suggests that *Sapium* may have had effective defences against native generalists when introduced, and its current palatable status is a relatively recent development. If this is true, then the historical avoidance of *Sapium* by native herbivores may be best explained by the Novel Defence Hypothesis, and the current evidence for a behavioural constraint simply represents a lag in herbivore response to an only recently palatable host plant. However, in the present study grasshoppers did not differentiate between Chinese and Texan seedlings, suggesting that grasshoppers have probably been able to feed on *Sapium* since it was introduced. Despite the plasticity of the behavioural constraint, it has apparently caused *M. angustipennis* to avoid *Sapium* for over a century at this site. If similar behavioural constraints are common among the native generalists at this site, then this may have indirectly facilitated *Sapium* invasion. Since the herbivores avoid *Sapium* for reasons independent of the defences produced by the plant, *Sapium* individuals that decrease their investment to defence would not suffer an increase in herbivory, but benefit by reinvesting resources toward growth and reproduction (Blossey & Nötzold, 1995).

Conclusions

This study has shown that low herbivory on *Sapium* in its introduced North American range is due at least in part to

the behavioural patterns of native generalist herbivores. *Sapium* could provide an additional abundant and conspicuous food source for generalists, yet has been avoided by them for the past 100 years. If this behavioural constraint is shared by other generalists, it may have allowed *Sapium* to reduce its investment to defence, increasing its ability to grow and reproduce without suffering the cost of higher herbivore loads (Siemann & Rogers, 2001).

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