Plant Ecology (2005) 181:57–68
DOI 10.1007/s11258-005-3029-6

# Herbivory tolerance and compensatory differences in native and invasive ecotypes of Chinese tallow tree (*Sapium sebiferum*)

William E. Rogers[1,2,*] and Evan Siemann[1]
[1]*Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005, USA;*
[2]*Current address: Department of Rangeland Ecology and Management, Texas A & M University, College Station, Texas 77843; *Author for correspondence (e-mail: wer@rice.edu; phone: +713-348-6338; fax: +713-348-5232)*

Received 15 July 2004; accepted in revised form 24 February 2005

*Key words:* Alien tree invasions, Grasshopper bioassay, Simulated defoliation, Woody encroachment

## Abstract

The Evolution of Increased Competitive Ability (EICA) hypothesis proposes that exotic plants may become superior competitors in their introduced ranges because they have evolved reduced defense allocation and increased growth in response to low herbivory. Long-term common garden studies with Chinese tallow tree (*Sapium sebiferum*), a problematic invader in the southeastern United States, support EICA predictions of invasive ecotypes displaying rapid growth with poorly defended leaves, whereas native ecotypes are slower growing and have nitrogen rich, highly defended leaves. We conducted two full-factorial experiments designed to assess the effects of leaf herbivory and soil fertility on growth of *Sapium* seedlings derived from seeds obtained in the species' native Chinese range and introduced range along the Texas Gulf Coast. The first was a field study employing simulated defoliation to examine herbivory tolerance, while the second was a pot study using grasshopper bioassays to measure the compensatory regrowth of native and introduced *Sapium* ecotypes. In accordance with EICA predictions, introduced Texas ecotypes compensated for mechanical and natural defoliation regardless of resource conditions while growth of native Chinese ecotypes was significantly reduced as a result of both simulated and natural herbivory damage. These results demonstrate that invasive *Sapium* ecotypes have a greater capacity to compensate for herbivory damage than native *Sapium* ecotypes. The differences between *Sapium* ecotypes are consistent with the mechanisms of EICA and other findings demonstrating that invasive ecotypes have become herbivory tolerant due to post-introduction changes in tissue quality.

## Introduction

Relatively small amounts of leaf herbivory can have major detrimental effects on plant growth, survival and competitive interactions (Hendrix 1988; Maschinski and Whitham 1989; Marquis 1992). The competitive advantage displayed by introduced plants over native plants is frequently attributed to differences in herbivore damage (Elton 1958; Crawley 1989; Tilman 1999). When non-native plants are introduced without specialist herbivores from their indigenous habitat they may gain a significant competitive advantage over native plants which often have greater numbers of herbivores (Strong et al. 1984; Schierenbeck et al. 1994; Yela and Lawton 1997). Phenotypic plasticity is also generally recognized as a key characteristic promoting the invasiveness of many exotic plants (Baker 1974; Alpert and Simms 2002; Sexton et al. 2002; Callaway et al. 2003; Parker et al. 2003). The

Enemy Release hypothesis proposes that exotic plants gain a competitive advantage over native plants by plastically allocating resources normally lost to enemies or construction of defenses toward growth or reproduction (Maron and Vila 2001; Keane and Crawley 2002; Mitchell and Power 2003; DeWalt et al. 2004).

An alternative to the Enemy Release hypothesis proposes that exotic plants evolve reduced allocation to defense and increased allocation to growth and reproduction due to an absence of herbivore selective pressures. The Evolution of Increased Competitive Ability (EICA) hypothesis (Blossey and Nötzold 1995), predicts that ecotypes from a plant's introduced range ('invasive ecotypes') will grow faster and/or produce more seeds, but be less well defended against enemies than ecotypes from its native range ('native ecotypes'). Because allocation to defense may be as costly as herbivore damage (Coley et al. 1985; Bazzaz et al. 1987; Simms 1992; Baldwin 1998), plants that escape their enemies in an introduced range should gain a selective benefit from decreasing their defensive investment. Conversely, the Enemy Release hypothesis holds that ecotype origin should not have a discernable effect on growth and vigor because plants plastically respond to their current ecological conditions.

To date, few manipulative studies have been performed to differentiate the EICA hypothesis from the Enemy Release hypothesis. An exception are field experiments that have revealed the Enemy Release hypothesis does not fully explain Chinese Tallow Tree (*Sapium sebiferum*) invasions in east Texas since the suppression of insect herbivores using chemical sprays caused significantly greater increases in the growth and survivorship of *Sapium* compared to native tree seedlings (Siemann and Rogers 2003a). Rather, common garden studies suggest that genetic differences in the growth and defense of invasive and native *Sapium* ecotypes are consistent with predictions of the EICA hypothesis (Siemann and Rogers 2001, 2003b, c; Rogers and Siemann 2004). Invasive ecotypes of *Sapium* from North America have significantly higher growth rates, earlier and greater seed production but lower foliar tannin concentrations than native *Sapium* ecotypes. Both ecotypes had uniformly low amounts of leaf area removed by insect herbivores in the introduced range (Siemann and Rogers 2001, 2003b). This outcome is not likely explained by a release from herbivory since both native and invasive ecotypes should have displayed a similar plastic phenotypic reallocation from defense to growth in the introduced range where enemies are absent (Maron and Vila 2001; Keane and Crawley 2002). Results from another long-term common garden study established in Hawaii reinforces this interpretation. In Hawaii, native *Sapium* ecotypes had less leaf damage and grew significantly larger than invasive Texas ecotypes, opposite our findings in the Texas common garden. This reversal of growth for the different ecotypes appears to be a result of introduced Asian herbivores in Hawaii feeding more heavily on poorly defended Texas ecotypes (Siemann and Rogers 2003c).

In order to gain new insights into ways that growth vs. defense allocation trade-offs may contribute to successful exotic plant species invasions we initiated a pair of experiments designed to assess herbivory tolerance and compensatory capacity of native and introduced *Sapium* ecotypes. The first study was a field experiment that manipulated soil fertility and leaf herbivory via mechanical defoliation on *Sapium* seedlings derived from seeds obtained in the species' native range in China and introduced range along the Texas Gulf Coast. Because simulated leaf damage does not discriminate between tissue chemistry in the same manner as natural herbivore choice, mechanical defoliation allowed us to measure herbivory tolerance and compensatory capacity of *Sapium* ecotypes independent of plant defenses. The EICA hypothesis predicts that native Chinese *Sapium* ecotypes invest significantly more resources in energetically expensive defenses than invasive Texas *Sapium* ecotypes that allocate resources to regrowth rather than ecologically costly secondary metabolites. Conversely, the Enemy Release hypothesis predicts that introduced plants become invasive by plastically responding to an absence of herbivores in their new range. As a result, the EICA hypothesis will be supported if Texas *Sapium* ecotypes exhibit markedly greater herbivory tolerance than Chinese *Sapium* ecotypes when damaged by simulated leaf herbivory. If the Enemy Release hypothesis is correct, both native and invasive *Sapium* should respond similarly to defoliation damage because there are no genetic differences between ecotype tissue quality. Fertilizer additions should increase the growth of both ecotypes, particularly fast growing Texas ecotypes, and should also lessen the negative effects of mechanical damage by stimulating the ability of both ecotypes to compensate for tissue losses.

In the second study, we further examined the compensatory regrowth ability of native and invasive *Sapium* seedlings by conducting herbivore bioassays using acridid grasshoppers in cage enclosures. Grasshoppers were caged with *Sapium* seedlings for 2 weeks and then the plants were allowed to regrow in the absence of herbivory for an additional 7 weeks in fertilized and unfertilized conditions. While the Enemy Release hypothesis predicts that both *Sapium* ecotypes will respond similarly to grasshopper herbivory, the EICA hypothesis predicts that the better defended Chinese *Sapium* ecotypes will experience less herbivory damage, but exhibit significantly reduced compensatory regrowth responses compared to Texas *Sapium* ecotypes after the herbivores are removed because their tissues are more costly to reconstruct. Because invasive Texas *Sapium* ecotypes allocate more resources to growth than defense if the EICA hypothesis is correct, they should be highly susceptible to grasshopper defoliation, but rapidly regrow lost tissue following herbivore removal. Again, fertilizer addition should increase seedling growth and improve the ability of both ecotypes to compensate for tissues lost to herbivory damage.

## Materials and methods

### *Focal species*

Chinese tallow tree (*Sapium sebiferum* (L.) Roxb., Euphorbiaceae) was originally introduced to the United States in 1772, but has only recently become a major woody invader in the southeastern United States (for detailed description see Siemann and Rogers 2003a). *Sapium* has been extensively planted throughout the southeastern United States for economic and aesthetic purposes (Scheld and Cowles 1981). It readily escapes cultivation and aggressively displaces native plants eventually converting a native ecosystem into a monotypic woodland (Jubinsky and Anderson 1996; Bruce et al. 1997).

### *Field experiment*

This experiment was conducted in a coastal tallgrass prairie at the University of Houston Coastal Center (UHCC) where the semitropical climate has at least a 250 day growing season, receives 1200 mm average annual rainfall, and soils are 40–60% clay. Mowed coastal prairie areas consist of perennial grasses and a diverse assemblage of other graminoids, perennial forbs and shrubs, but unmowed areas are rapidly invaded and have been primarily converted to *Sapium* woodlands (Bruce et al. 1997; Siemann and Rogers 2003a).

Seeds of both native Chinese and invasive Texas *Sapium* trees were germinated in a greenhouse on the Rice University campus during April–May 2001. Seeds were obtained from numerous trees at the South China Botanical Garden in Guangzhou, China (‘Chinese ecotype’ and ‘native *Sapium* ecotype’ henceforth) and collected from naturalized *Sapium* trees in Galveston County, Texas (‘Texas ecotype’ and ‘invasive *Sapium* ecotype’ henceforth) in autumn 2000. We germinated the seeds in single-celled, 100 ml containers (Stuewe and Sons, Inc., Corvallis, OR) filled with field soil collected from a UHCC grassland near the study site. Once the seedlings had primary leaves, they were placed beneath a 50% shade cloth outdoors for 4 weeks. On 25 May 2001, we selected 32 native China ecotype *Sapium* seedlings and 32 invasive Texas ecotype *Sapium* seedlings and individually transplanted them in randomly assigned 1 $m^2$ plots in a recently mowed prairie. Earlier germination of China seedlings resulted in their starting size being larger than Texas seedlings. We transplanted each *Sapium* seedling in the center of alternating plots so that all seedlings were a minimum of 2 m apart. The plots were periodically watered using ground soaking hoses to minimize transplant mortality and drought stress. We sprayed Esfenvalerate (tradename: Asana XL, DuPont Agricultural Products, Wilmington, DE) on the vegetation and *Sapium* seedlings monthly to prevent uncontrolled background herbivory. Previous studies confirm this pesticide is not toxic to *Sapium* or *Schizachyrium*, the dominant prairie grass at this site (Siemann and Rogers 2003a). Eighteen seedlings (4 China, 14 Texas) died and were replaced during the first month after transplanting. The later germination and subsequent smaller starting size of Texas seedlings likely made them more susceptible to transplanting stress.

We initiated the 15-week experiment on 5 July 2001 (time 0) at which time we recorded initial *Sapium* stem heights, basal diameters and leaf numbers. We measured stem height of each seedling from the soil surface to the apical meristem to the nearest millimeter and measured stem diameter at the soil surface with a digital caliper to the nearest 0.1 mm. We also collected visual estimates of prairie plant cover in the plots. A full-factorial experimental design was employed by randomly assigning simulated leaf herbivory and fertilizer addition treatments to plots with transplanted seedlings from each *Sapium* ecotype. Each treatment combination was replicated eight times.

Herbivore defoliation was simulated by removing the distal half of every full leaf blade with scissors during weeks 5 and 9. The scissors were sterilized with an alcohol wipe after defoliating each seedling to prevent the spread of disease or secondary chemicals. Clipped leaves that remained on seedlings until week 9 were cut in half a second time as were all newly added leaves. The single uppermost leaf of each seedling was excluded during each simulated herbivory event to protect the apical meristem and avoid affecting branch dynamics (Marquis 1992). This type of simulated leaf herbivory can adequately represent decreased leaf area and mass loss experienced by herbivore damaged tree seedlings despite well established limitations (Hendrix 1988; Marquis 1992; Stowe et al. 2000; Tiffin and Inouye 2000) and in some instances can provide greater accuracy and precision than experiments using natural damage (e.g., Lehtila 2003). Leaf clippings from each seedling were dried and weighed.

Supplemental nutrients were 3 g nitrogen, 1 g phosphorus, and 2 g potassium per $m^2$ per application added as dry 15-5-10 NPK fertilizer pellets during weeks 1, 7, and 12. Thus, a total of 9 g nitrogen, 3 g phosphorus and 6 g potassium per $m^2$ were added in the fertilized treatments.

On 16 October, the end of 15 weeks, we measured final *Sapium* stem heights, basal diameters, and the number of leaves on each seedling. We visually estimated final prairie vegetation cover in each plot. *Sapium* stems were clipped at the soil base and leaves were clipped from stems. Roots were not harvested because we have been unsuccessful in obtaining accurate belowground mass measures when extracting root tissues from these heavy clay soils. A 0.1 $m^2$ frame was used to clip aboveground prairie vegetation in each plot and was sorted into graminoid, forb and woody functional groups. *Sapium* leaves and stems and clipped prairie plants were dried at 60 °C for at least 72 h and weighed separately.

### *Grasshopper bioassay experiment*

We performed an additional experiment to examine the ability of native and invasive *Sapium* ecotypes to compensate for natural insect herbivory with different levels of fertility. The use of real herbivores can also provide a means of evaluating the effectiveness and realism of simulated herbivory studies. The final design created a full-factorial combination of ecotype, herbivory and fertilization treatments.

Seeds of native Chinese and invasive Texas *Sapium* trees that germinated in the greenhouse during June 2002 were maintained throughout the summer in topsoil filled containers beneath an outdoor shade cloth in the courtyard of the Rice University greenhouse. On 26 August, 48 *Sapium* seedlings (24 of each ecotype) were transplanted into 7.65 l pots filled with commercially available topsoil and returned to a single bench in the greenhouse. We measured the stem height of each transplanted seedling. Pots were watered daily and rotated among positions in the greenhouse weekly.

On 10 September, we sowed pots with 50 $g/m^2$ (1.5 g per pot) of annual ryegrass seed (*Lolium multiflorum* Lam.). Ryegrass seeds were covered with 5 mm of topsoil and germinated within 3 days of sowing. The ryegrass was added to increase the competitive environment experienced by the *Sapium* seedlings and provided generalist grasshoppers an alternative food to *Sapium* foliage.

On 24 September, aluminum mesh cages were erected around each seedling. Cages were cylinders of aluminum window screening (75 cm high, 300 $cm^2$, 1.6 mm mesh size aluminum) joined at the base to aluminum flashing that was fitted 1 cm into the soil in the pot. We have used these cages successfully in other grasshopper bioassay studies (Siemann and Rogers 2003b; Lankau et al. 2004). Chinese and Texas *Sapium* seedlings were randomly assigned grasshopper herbivory treatments. Two grasshoppers (*Melanoplus angustipennis* Dodge) were added to the open top of each cage before folding the mesh and fastening it closed with metal binder clips. Control pots did not receive grasshoppers, but still had cages erected around the seedlings to avoid differences in light availability and microclimate.

Melanopline (Orthoptera: Acrididae: Melanoplinae) grasshoppers are generalist feeders that typically consume a mixed diet of forbs, woody plants and grasses (Ueckert and Hansen 1971). The most abundant species in this subfamily in east Texas coastal tallgrass prairie is the Narrow-winged Sand Grasshopper, *M. angustipennis* (Lankau et al. 2004). 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). The grasshoppers used in this study were captured by sweep netting at the coastal prairie research station described for the field experiment. All grasshoppers were maintained for 2 days in temporary laboratory terrariums with clipped prairie vegetation prior to stocking them in bioassay cages. Grasshoppers were left in the cages for two weeks and removed on 7 October. The cages were also removed from both herbivory and control pots at this time. We visually estimated the average percent area damaged per leaf. This method has been shown to be a good estimation of leaf removal when compared to digital leaf scans (Siemann and Rogers 2001, 2003a; Lankau et al. 2004).

On 9 October, we added fertilizer as 6 g nitrogen, 2 g phosphorus, 3 g potassium per $m^2$ to half of the pots. Seedlings receiving fertilizer that were not exposed to herbivores were randomly assigned, whereas pots that contained herbivores were paired with respect to the amount of damage the seedling experienced (highest to lowest). For instance, two Texas *Sapium* seedlings were 100% defoliated by grasshoppers, one was randomly assigned to receive a fertilizer amendment while the other was maintained as a control. Similarly, the two Texas *Sapium* seedlings that received the least amount of damage when exposed to herbivores (30% defoliation each) were paired and one was randomly assigned to receive a fertilizer amendment while the other was maintained as a control. The same procedure was followed for defoliated Chinese *Sapium* seedlings.

On 25 November, 13 weeks from the start of the experiment and 7 weeks after grasshoppers were removed, we measured final stem height and the number of leaves on each seedling. *Sapium* and *Lolium* shoots were clipped at the soil surface and bagged separately. Roots were gently washed from the soil. None of the tree seedlings appeared to be growth-limited by rooting space. *Sapium* and *Lolium* roots were easily distinguished and carefully separated except for very fine roots. *Lolium* roots were not retained. Harvested plant tissues were dried at 60 °C and weighed separately.

### *Data analyses*

Logistic regression was used to assess treatment effects on *Sapium* survival. Seedlings that died were excluded from growth rate and mass analyses. *Sapium* growth rates, ln(final measurement/initial measurement), were calculated for stem height in both studies and for basal stem diameter in the field experiment. This calculation also transformed the data to meet statistical assumptions of analysis of variance (ANOVA). We used ANOVA to compare *Sapium* growth rates and plant mass among leaf damage treatments, fertilizer addition and their interaction (SAS Institute, Cary, NC, USA). When necessary, starting stem diameter was used as a covariate for the field experiment and starting stem height was used as a covariate for the grasshopper bioassay experiment in mass analyses to control for differences in initial seedling size. Percent of leaf area removed per seedling in the grasshopper bioassay experiment (percentage leaf area damage * number of damaged leaves/total number of leaves) was calculated for seedlings exposed to herbivores and arcsine transformed to satisfy ANOVA assumptions. Mass data were square-root transformed to meet statistical assumptions of ANOVA. Because of size differences between ecotypes we analyzed each *Sapium* ecotype with separate three-way factorial analyses (*sensu* Shaver and Chapin 1980; Mitchell et al. 1992). Mass data were back-transformed and presented as means (+1 SE).

## Results

### *Field experiment*

After 15 weeks, five of the 64 transplanted *Sapium* seedlings lost their leaves and were considered dead. There were no statistically significant effects of ecotype, nutrients or simulated leaf herbivory on survival as determined by logistic regression ($r^2 = 0.442, p > 0.05$). *Sapium* has a notable ability to sprout new leaves from a seemingly dead stem throughout many years of growth (William Rogers, personal observation; Siemann and Rogers 2003a). Consequently, seedlings designated 'dead' could potentially have resprouted after a longer time.

Stem height of Chinese *Sapium* ecotypes was significantly greater than stem height of Texas *Sapium* ecotypes at the initiation of the study ($F_{1,62} = 14.52, p = 0.0003$), presumably due to the earlier germination time. As a result, mean leaf mass clipped from Chinese ecotype seedlings was modestly greater than mass clipped from Texas ecotype seedlings in the first simulated herbivory trial ($F_{1,27} = 4.66$, $p = 0.04$). There was no difference between mean leaf mass clipped from the different ecotypes in the second simulated herbivory trial ($F_{1,27} = 2.23$, $p = 0.15$). Fertilizer had no significant effect on the amount of leaf mass clipped in either the first ($F_{1,27} = 0.08$, $p = 0.78$) or second simulated herbivory trials ($F_{1,27} = 0.17, p = 0.68$).

Additional nutrients significantly increased height growth rate of both Texas ($F_{1,23} = 10.72$, $p = 0.003$) and Chinese ($F_{1,28} = 11.10, p = 0.002$) seedlings (Table 1). Height growth rates of Texas ($F_{1,23} = 0.93$, $p = 0.345$) and Chinese ($F_{1,28} = 0.29$, $p = 0.594$) ecotypes were not affected by simulated leaf herbivory (Table 1). There was a trend for simulated leaf herbivory to increase the basal stem diameter growth rate of Texas ecotypes ($F_{1,23} = 4.17$, $p = 0.053$) and a significant interaction between additional nutrients and mechanical defoliation ($F_{1,23} = 4.92, p = 0.037$) stimulating an increase of basal stem diameter growth rate of Texas *Sapium* ecotypes (Table 1A). Basal diameter growth rate of Chinese ecotypes was unaffected by simulated herbivory ($F_{1,28} = 0.66$, $p = 0.425$) or fertilizer ($F_{1,28} = 0.01$, $p = 0.923$) treatments (Table 1B). Additional nutrients significantly increased the leaf mass of Texas ecotypes ($F_{1,22} = 10.11$, $p = 0.004$, Figure 1). There was no effect of nutrients on leaf mass ($F_{1,25} = 0.51$, $p = 0.480$) or stem mass ($F_{1,25} = 0.07, p = 0.796$) of Chinese ecotypes (Table 2B, Figure 1).

Although simulated leaf herbivory had no effect on the leaf mass ($F_{1,22} = 0.05, p = 0.829$) or stem mass ($F_{1,22} = 0.38$, $p = 0.542$) of Texas ecotypes (Figure 1), simulated leaf herbivory significantly decreased both leaf ($F_{1,25} = 5.91$, $p = 0.022$) and stem mass ($F_{1,25} = 11.03$, $p = 0.003$) of Chinese ecotype seedlings (Table 1, Figure 1). Experimental treatments had no significant effects on prairie vegetation cover or plant mass (data not shown).

*Table 1.* Means (+1 SE) and analysis of (co)variance (ANOVA) for growth parameters of (A) invasive and (B) native *Sapium* seedlings planted in east Texas coastal tallgrass prairie in a full-factorial experimental design with NPK fertilizer addition and simulated leaf herbivory treatments.

| | No added fertilizer | | NPK added | | ANOVA | | |
|---|---|---|---|---|---|---|---|
| | No damage ($n = 8$) | Herbivory ($n = 8$) | No damage ($n = 6$) | Herbivory ($n = 5$) | NPK (N) | Herb (H) | N × H |
| (A) Texas ecotype | | | | | | | |
| Height growth rate | 0.374 + 0.09 | 0.488 + 0.06 | 0.672 + 0.10 | 0.713 + 0.05 | ** | ns | ns |
| Diameter growth rate | 0.355 + 0.06 | 0.345 + 0.03 | 0.286 + 0.08 | 0.525 + 0.05 | – | ns | * |
| Leaf dry mass (g) | 0.053 + 0.02 | 0.056 + 0.03 | 0.148 + 0.07 | 0.193 + 0.11 | ** | ns | ns |
| Stem dry mass (g) | 0.154 + 0.07 | 0.212 + 0.11 | 0.235 + 0.11 | 0.299 + 0.20 | ns | ns | ns |
| | No added fertilizer | | NPK added | | ANOVA | | |
| | No damage ($n = 8$) | Herbivory ($n = 8$) | No damage ($n = 8$) | Herbivory ($n = 8$) | NPK (N) | Herb (H) | N × H |
| (B) Chinese ecotype | | | | | | | |
| Height growth rate | 0.456 + 0.05 | 0.319 + 0.07 | 0.577 + 0.08 | 0.642 + 0.05 | ** | ns | ns |
| Diameter growth rate | 0.376 + 0.05 | 0.254 + 0.05 | 0.301 + 0.06 | 0.339 + 0.05 | ns | ns | ns |
| Leaf dry mass (g) | 0.295 + 0.11 | 0.102 + 0.04 | 0.220 + 0.09 | 0.251 + 0.08 | ns | ** | ns |
| Stem dry mass (g) | 0.567 + 0.19 | 0.367 + 0.11 | 0.415 + 0.19 | 0.452 + 0.11 | ns | ** | ns |

Data are presented as growth rates, ln(final mm/initial mm), and back-transformed mass.
*p*-value: ns – not significant; ≤ 0.1; * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001; **** ≤ 0.0001.

*Table 2.* Means (+1 SE) and analysis of (co)variance (ANOVA) for growth parameters of (A) invasive Texas and (B) native Chinese *Sapium* seedlings planted in pots in a full-factorial experimental design with NPK fertilizer addition and grasshopper herbivory treatments.

| | No added fertilizer | | NPK added | | ANOVA | | |
|---|---|---|---|---|---|---|---|
| | No damage ($n = 6$) | Herbivory ($n = 6$) | No damage ($n = 6$) | Herbivory ($n = 6$) | NPK (N) | Herb (H) | N × H |
| (A) Texas ecotype | | | | | | | |
| Height growth rate | 0.202 + 0.06 | −0.025 + 0.08 | 0.149 + 0.03 | 0.025 + 0.04 | ns | ** | ns |
| Shoot mass (g) | 1.563 + 0.31 | 1.409 + 0.39 | 1.772 + 0.27 | 1.503 + 0.54 | ns | ns | ns |
| Root mass (g) | 1.904 + 0.17 | 1.445 + 0.31 | 2.053 + 0.33 | 1.598 + 0.45 | ns | ns | ns |
| (B) Chinese ecotype | | | | | | | |
| Height growth rate | 0.259 + 0.04 | 0.077 + 0.04 | 0.264 + 0.04 | 0.049 + 0.02 | ns | **** | ns |
| Shoot mass (g) | 2.43 + 0.34 | 2.005 + 0.59 | 2.621 + 0.36 | 2.176 + 0.67 | ns | * | ns |
| Root mass (g) | 2.512 + 0.26 | 1.598 + 0.38 | 2.280 + 0.35 | 1.662 + 0.48 | ns | ** | ns |

Mean percentage leaf area removed (+1 SE) by grasshoppers was 53.1 + 22.1% for Texas *Sapium* ecotypes and 38.0 + 10.6% for Chinese *Sapium* ecotypes. Data are presented as height growth rate, ln(final mm/initial mm), and back-transformed mass.
$p$-value: ns – not significant; * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001; **** ≤ 0.0001.

### *Grasshopper bioassay experiment*

All 48 *Sapium* seedlings survived the 13 week grasshopper bioassay experiment. Four seedlings (3 Texas ecotypes and 1 Chinese ecotype) were completely defoliated (>99%) and considerable apical meristem damage was observed on several seedlings. Nevertheless, all damaged seedlings sprouted new leaves from existing stems shortly after herbivores were removed. Mean percent leaf area removed by grasshoppers was higher for Texas than Chinese *Sapium* ecotypes (53.1 + 22.1% and 38.0 + 10.6%, respectively), but was not statistically different ($F_{1,22} = 0.67$, $p = 0.42$). While we have removed similar amounts of leaf area in simulated herbivory experiments (Rogers and Siemann 2002, 2003), the estimated removal in this grasshopper bioassay is likely conservative due to grasshoppers continually consuming growing tissues compared to a single defoliation event like mechanical leaf damage.

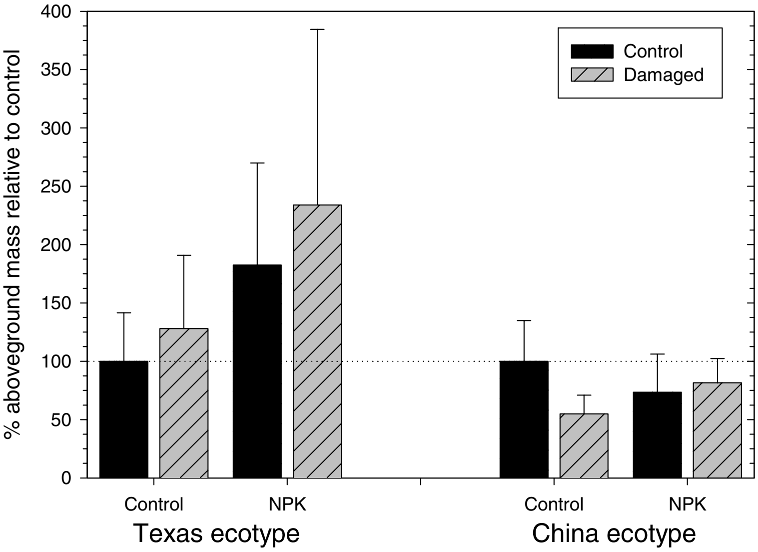

*Figure 1.* Percentage of *Sapium* leaf and stem (means +1 SE) mass of Texas and Chinese ecotype seedlings grown in coastal tallgrass prairie while exposed to mechanical defoliation and fertilizer amendment (NPK) treatments relative to undamaged, unfertilized control seedlings (100%).

Starting seedling stem height did not statistically differ between Texas and Chinese ecotypes ($F_{1,40} = 0.879, p = 0.354$), likely because germination times for the two ecotypes more closely corresponded in spring 2002 (Evan Siemann, personal observation). However, starting stem height was significantly larger for seedlings that were to be exposed to grasshopper herbivores ($F_{1,40} = 6.569$, $p = 0.014$). Height growth rate of both Texas ecotypes ($F_{1,20} = 9.00$, $p = 0.007$) and Chinese ecotypes ($F_{1,20} = 27.44$, $p < 0.0001$) was significantly reduced by grasshopper consumption, but fertilization did not affect the growth rate for either Texas ($F_{1,20} = 0.00, p = 0.982$) or Chinese ($F_{1,20} = 0.09$, $p = 0.764$) *Sapium* seedlings (Table 2). Grasshopper herbivory did not affect shoot ($F_{1,19} = 0.42$, $p = 0.525$) or root mass ($F_{1,19} = 1.84, p = 0.191$) of Texas ecotypes (Table 2A), whereas herbivory significantly reduced shoot mass ($F_{1,19} = 6.50$, $p = 0.020$) and root mass ($F_{1,19} = 9.27, p = 0.007$) of Chinese ecotypes (Table 2B). Fertilization did not affect the shoot mass or root mass of Texas ($F_{1,19} = 0.05, p = 0.830$; $F_{1,19} = 0.16, p = 0.690$, respectively) or Chinese ($F_{1,19} = 0.07$, $p = 0.801$; $F_{1,19} = 0.44$, $p = 0.517$, respectively) ecotypes (Table 2).

## Discussion

Invasive Texas *Sapium* ecotypes compensated for high levels of mechanical leaf damage in the field study and also compensated for tissue lost to grasshopper herbivory in bioassay trials. Conversely, defoliated native Chinese *Sapium* ecotypes exhibited decreased growth and reduced mass relative to undamaged control seedlings in both experiments. These results provide better support for the Evolution of Increased Competitive Ability hypothesis than the Enemy Release hypothesis. The Enemy Release hypothesis predicts that native and introduced ecotypes of an exotic plant species will display considerable phenotypic plasticity and respond similarly when grown in a common environment. With reduced damage, resources normally lost to enemies may be plastically allocated to growth and/or reproduction, whereas with increased damage the ecotypes may display a range of responses depending on whether the species is herbivory tolerant or herbivory resistant. Regardless, the Enemy Release hypothesis predicts that native and introduced ecotypes should respond similar to each other because they share the same genetic characteristics for tissue quality. Our results do not support this, but rather are consistent with EICA predictions that invasive Texas *Sapium* ecotypes display herbivory tolerant characteristics and allocate resources to regrowth while Chinese *Sapium* ecotypes exhibit herbivory resistant traits and are less able to compensate for herbivore damage.

A trade-off between herbivory resistance and herbivory tolerance mechanisms is well established in ecological theory (van der Meijden et al. 1988; Herms and Mattson 1992; Simms 1992; Pilson 2000). Herbivory tolerant plants typically possess low quality tissues that are rapidly replaced following defoliation (Haukioja and Koricheva 2000; Stowe et al. 2000). Weis et al. (2000) define tolerance as the ability of a plant ecotype to maintain growth and fitness despite tissue damage. Compensatory capacity, the ability of a damaged plant to regrow relative to an undamaged control plant, is a commonly used measure of assessing herbivory tolerance. Herbivory resistant plants invest resources and energy that would otherwise be used for growth or reproduction into herbivore deterrents (Fineblum and Rausher 1995; Mauricio 2000; Strauss et al. 2002). However, because defenses are costly to produce and maintain, mechanical leaf damage that does not discriminate between tissue chemistry is likely to have a greater negative effect on herbivory resistant than herbivory tolerant plants. Results from this study suggest that native Chinese *Sapium* ecotypes are herbivory resistant while invasive Texas *Sapium* ecotypes are herbivory tolerant.

Other researchers have suggested that an isolated population of introduced plants may lose resistance to herbivory over time (Blossey and Nötzold 1995; Daehler and Strong 1997; Willis et al. 1999; Mack et al. 2000; Mooney and Cleland 2001). Nonetheless, reductions in defense will lead to greater competitive ability only when the additional costs of herbivore damage do not exceed the reduced costs of defense (Coley et al. 1985; Bazzaz et al. 1987; Maschinski and Whitham 1989; Mauricio 1998; Agrawal 2000). This phenomenon may be particularly relevant to exotic plant species that have escaped their native specialist herbivores and are unrecognized as a suitable food source by local generalist herbivores in their new habitat

(Lankau et al. 2004). Introduced *Sapium* ecotypes lack high concentrations of energetically expensive chemical deterrents found in native ecotypes, yet do not suffer appreciable herbivore damage in their introduced range (Siemann and Rogers 2001). This novel combination of low herbivory despite low investment in defense has increased the competitive ability of Texas *Sapium* and potentially contributes to its invasiveness.

Our results showing the compensatory capacity of Texas *Sapium* ecotypes to mechanical defoliation are likely to be conservative estimates of its ability to tolerate damage. A criticism of simulated herbivory studies is that they often remove more biomass than herbivores in natural conditions and, thus, greatly exaggerate the severity of damage (Hendrix 1988; Tiffin and Inouye 2000). We have conducted several other studies examining herbivory tolerance of Texas *Sapium* when exposed to different modes and intensities of defoliation in a variety of environmental conditions (Rogers et al. 2000; Rogers and Siemann 2002, 2003). In all instances, invasive Texas *Sapium* ecotypes exhibited a marked short-term tolerance of simulated herbivory damage. Moreover, since compensatory responses of many long-lived woody plants to herbivore damage are likely to become manifest and extend for several years beyond the time of defoliation (Hendrix 1988; Obeso 1993; Sacchi and Conner 1999; Haukioja and Koricheva 2000), rapid compensation observed for invasive Texas *Sapium* ecotypes further demonstrates its ability to survive and regrow after experiencing considerable levels of tissue loss.

To our knowledge, this is the first comparative study showing differences in the ability of native and invasive ecotypes to tolerate foliar herbivory damage. Van Kleunen and Schmid (2003) recently conducted a similar simulated herbivory study with *Solidago canadensis*, but did not find any significant demographic differences in the herbivory tolerance of native and invasive ecotypes. Bossdorf et al. (2004) demonstrated that *Alliaria petiolata* ecotypes from the introduced range were less defended than native ecotypes, but there were no significant differences in herbivory tolerance between the native and introduced populations. While it is possible that over time Chinese ecotypes in our current study would compensate for the mechanical and grasshopper herbivory damage imposed, the rapid compensation exhibited by Texas ecotypes emphasizes differences in herbivore tolerance and growth between native and invasive *Sapium*. Moreover, while both *Sapium* ecotypes displayed increased growth rates and damaged plants appeared to increase plant mass in response to nutrient amendments, damaged Texas ecotypes exhibited a strong overcompensating response in diameter growth rate when fertilizer was added. The ability to readily exploit available nutrients and convert them into plant mass following damage is characteristic of rapidly growing plant species and further evidence of Texas ecotypes fast growing, herbivory tolerant life history.

An alternative explanation for our results is that negative effects of damage were observed for Chinese ecotype seedlings because they were larger than Texas ecotype seedlings and had more leaf mass removed in one of the simulated herbivory trials. We do not believe this accurately accounts for our findings. A similar argument could claim that if Texas ecotypes were larger than Chinese ecotypes, the larger seedlings have greater root reserves and are better able to compensate for leaf losses to herbivory. Rather, several lines of research suggest that woody tree seedlings are most vulnerable when they are small during early life history stages (Fenner 1987; Meiners and Handel 2000). The results presented here demonstrate compensation in Texas *Sapium* ecotypes and negative effects of damage on the growth of Chinese *Sapium* ecotypes. We have also recently reported that Texas *Sapium* ecotypes tolerate simulated root herbivory more effectively than Chinese *Sapium* ecotypes (Rogers and Siemann 2004). These patterns of herbivory tolerance are also consistent with other short-term studies examining herbivory resistance (Siemann and Rogers 2003b) and long-term common garden studies comparing native and invasive *Sapium* ecotypes (Siemann and Rogers 2001, 2003c). Repeatedly, we have found results supporting that invasive Texas *Sapium* ecotypes have undergone a shift away from possessing well-defended tissues found in native *Sapium* ecotypes to producing relatively inexpensive tissues that grow rapidly.

In a separate study, Siemann and Rogers (2003b) used grasshopper bioassays with paired potted *Sapium* seedlings derived from native Chinese and invasive Texas ecotypes to show significant herbivore preferences for the foliage of invasive Texas *Sapium* seedlings when offered a choice, thereby suggesting that native *Sapium* ecotypes were more resistant to herbivores because they contain greater amounts of defense chemicals. In the companion study reported here, grasshoppers were stocked with a single *Sapium* ecotype and the seedlings were allowed 7 weeks to regrow after grasshoppers were removed. Although the height growth rate was significantly reduced by grasshopper herbivory, presumably due to the considerable amount of meristem damage that occurred, Texas *Sapium* ecotypes were able to compensate for herbivory damage such that there was no statistical difference between the final mass of damaged and undamaged seedlings. Since height growth rate is calculated using stem length measurements from the soil surface to the tallest meristem, plants that lost their apical dominance due to grasshopper consumption would expectedly have reduced growth rates. Comparatively, after 7 weeks of regrowth, height growth rate, above- and belowground plant mass of Chinese *Sapium* ecotypes defoliated by grasshoppers were all significantly reduced compared to undamaged plants. Despite higher amounts of grasshopper herbivory damage, Texas *Sapium* ecotypes displayed greater compensatory regrowth than Chinese *Sapium* ecotypes.

It is important to recognize that the two leading hypotheses for the success of exotic species, Enemy Release and EICA, share a central premise. Evolution of invasiveness can only occur if exotic plants first experience an ecological release from enemies in their introduced range that strongly alters selection pressures and leads to genetic shifts away from defense allocation and toward greater growth and reproduction. The Enemy Release hypothesis predicts that plants become invasive because they have escaped the specialist pest and pathogens from their native range. Reestablishing these feeding relationships by introducing specialist enemies into the invasive range is the central premise of effective biological control strategies. The EICA hypothesis predicts that while genetic changes in introduced species may contribute to their ecological success, it may also increase their susceptibility to herbivores introduced from their native range. It is possible that this explains the dramatic success of certain biological control efforts. Effective biological control may not only result from a reestablishment of feeding relationships with native specialist herbivores, but also be attributable to a genetic shift away from chemical deterrents in the host plant, thereby increasing susceptibility to native herbivores.

The compensatory capacity of Texas *Sapium* ecotypes observed in the studies reported here likely would not be sustainable in situations where herbivores were continuously feeding over multiple growing seasons. However, Lankau et al. (2004) have shown that despite being susceptible to a dominant herbivore in areas it invades, Texas *Sapium* ecotypes are largely avoided due to behavioral barriers. As a result, these invasive *Sapium* ecotypes are not likely to sustain heavy amounts of continuous damage in the short term. Nonetheless, the insights reported here into the herbivory tolerance of invasive Texas ecotype seedlings compared to the decreased growth of defoliated native Chinese ecotype seedlings provides further evidence of differences between native and invasive *Sapium* ecotypes that is consistent with the EICA hypothesis and will prove useful for land managers attempting to devise control strategies for this and other problematic invasive species.

## Acknowledgements

Brad Butterfield, Jacob Ferris, Vikki Keener, Rick Lankau, and Danny Mee provided technical assistance; Xang Yanci and Jie Lin helped obtain Chinese seeds; Saara DeWalt and two anonymous reviewers made valuable comments on the manuscript, and the University of Houston Coastal Center gave permission to collect seeds and establish the field study. The US National Science Foundation (DEB-9981654) provided support for this research.

## References

Agrawal A.A. 2000. Benefits and costs of induced plant defense for *Lepidium Virginicum* (Brassicaceae). Ecology 81: 1804–1813.

Alpert P. and Simms E.L. 2002. The relative advantage of plasticity and fixity in different environments: when is it good for a plant to adjust? Evol. Ecol. 16: 285–297.

Baldwin I. 1998. Jasmonate-induced responses are costly but benefit plants under attack in native populations. Proc. Natl. Acad. Sci. USA 95: 8113–8118.

Baker H.G. 1974. The evolution of weeds. Annu. Rev. Ecol. Syst. 5: 1–24.

Bazzaz F.A., Chiariello N.R., Coley P.D. and Pitelka L.F. 1987. Allocating resources to reproduction and defense. BioScience 37: 58–67.

Blossey B. and Nötzold R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J. Ecol. 83: 887–889.

Bossdorf O., Schröder S., Prati D. and Auge H. 2004. Palatability and tolerance to simulated herbivory in native and introduced populations of *Alliaria petiolata* (Brassicaceae). Am. J. Bot. 91: 856–862.

Bruce K.A., Cameron G.N., Harcombe P.A. and Jubinsky G. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese Tallow Tree, *Sapium sebiferum* (L.) Roxb. Nat. Areas J. 17: 255–260.

Callaway R.M., Pennings S.C. and Richards C.L. 2003. Phenotypic plasticity and interactions among plants. Ecology 84: 1115–1128.

Coley P.D., Bryant J.P. and Chapin F.S. 1985. Resource availability and plant antiherbivore defense. Science 230: 895–899.

Crawley M.J. 1989. Chance and timing in biological invasions. In: Drake J.A., Mooney H.A., di Castri F., Groves R.H., Kruger F.J., Rejmanek M. and Williamson M.W. (eds), Biological Invasions. John Wiley and Sons, New York, pp. 407–424.

Daehler C. and Strong D.R. 1997. Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora)* after a century of herbivore-free growth. Oecologia 110: 99–108.

DeWalt S.J., Denslow J.S. and Ickes K. 2004. Natural enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85: 471–483.

Elton C.S. 1958. The Ecology of Invasion by Plants and Animals. Chapman and Hall, London.

Fenner M. 1987. Seedlings. Can. J. Bot. 106: 35–47.

Fineblum W.L. and Rausher M.D. 1995. Tradeoff between resistance and tolerance to herbivore damage in a morning glory. Nature 377: 517–520.

Hendrix S.D. 1988. Herbivory and its impact on plant reproduction. In: Lovett-Doust J. and Lovett-Doust L. (eds), Plant Reproductive Ecology. Oxford Press, New York, pp. 246–263.

Herms D.A. and Mattson W.J. 1992. The dilemma of plants: to grow or to defend. Quart. Rev. Biol. 67: 283–335.

Haukioja E. and Koricheva J. 2000. Tolerance to herbivory in woody vs. herbaceous plants. Evol. Ecol. 14: 551–562.

Jubinsky G. and Anderson L.C. 1996. The invasive potential of Chinese Tallow-tree *(Sapium sebiferum* Roxb.) in the southeast. Castanea 61: 226–231.

Keane R.M. and Crawley M.J. 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17: 164–170.

Lankau R.A., Rogers W.E. and Siemann E. 2004. Constraints on the utilization of the invasive Chinese Tallow Tree (*Sapium sebiferum)* by generalist native herbivores in coastal prairies. Ecol. Entomol. 29: 66–75.

Lehtila K. 2003. Precision of herbivore tolerance experiments with imposed and natural damage. Evolution 57: 677–680.

Mack R.N., Simberloff D., Lonsdale W.M., Evans H., Clout M. and Bazzaz F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10: 689–710.

Marquis R.J. 1992. The selective impact of herbivores. In: Fritz R.S. and Simms E.L. (eds), Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics. University of Chicago Press, Chicago, pp. 301–325.

Maron J.L. and Vila M. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses Oikos 95: 361–373.

Maschinski J. and Whitham T. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. Am. Natural. 134: 1–19.

Mauricio R. 1998. Costs of resistance to natural enemies in field populations of the annual plant *Arabidopsis thaliana*. Am. Natural. 151: 20–28.

Mauricio R. (2000) Natural selsection and the joint evolution of tolerance and resistance as plant defenses, Evol. Ecol. 14: 491–507.

Meiners S.J. and Handel S.N. 2000. Additive and nonadditive effects of herbivory and competition on tree seedling mortality, growth, and allocation. Am. J. Bot. 87: 1821–1826.

Mitchell C.E. and Power A.G. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421: 625–627.

Mitchell P., Arthur W. and Farrow M. 1992. An investigation of population limitation using factorial experiments. Ecology 61: 591–598.

Mooney H.A. and Cleland E.E. 2001. The evolutionary impact of invasive species. Proc. Natl. Acad. Sci. USA 98: 5446–5451.

Obeso J.R. 1993. Does defoliation affect reproductive output in herbaceous perennials and woody plants in different ways? Funct. Ecol. 7: 150–155.

Parker I.M., Rodriguez J. and Loik M.E. 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. Conserv. Biol. 17: 59–72.

Pilson D. 2000. The evolution of plant response to herbivory: simultaneously considering resistance and tolerance in *Brassica rapa*. Evol. Ecol. 14: 457–489.

Rogers W.E., Nijjer S., Smith C.L. and Siemann E. 2000. Effects of resources and herbivory on leaf morphology and physiology of Chinese tallow (*Sapium sebiferum*) tree seedlings. Tex. J. Sci. 52S: 43–56.

Rogers W.E. and Siemann E. 2002. Effects of simulated herbivory and resource availability on native and invasive exotic tree seedlings. Basic Appl. Ecol. 3: 297–307.

Rogers W.E. and Siemann E. 2003. Effects of simulated herbivory and resources on Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasion of native coastal prairie. Am. J. Bot. 90: 243–249.

Rogers W.E. and Siemann E. 2004. Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree. J. Appl. Ecol. 41: 561–570.

Sacchi C.F. and Conner E.F. 1999. Changes in reproduction and architecture in flowering dogwood, *Cornus florida*, after attack by dogwood club gall, *Resseliella clavula*. Oikos 86: 138–146.

Scheld H.W. and Cowles J.R. 1981. Woody biomass potential of the Chinese Tallow Tree. Econ. Bot. 35: 391–397.

Schierenbeck K.A., Mack R.N. and Sharitz R.R. 1994. Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. Ecology 75: 1661–1672.

Sexton J.P., McKay J.K. and Sala A. 2002. Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. Ecol. Appl. 12: 1652–1660.

Shaver G.R. and Chapin F.S. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61: 662–675.

Siemann E. and Rogers W.E. 2001. Genetic differences in growth of an invasive tree species. Ecol. Lett. 4: 514–518.

Siemann E. and Rogers W.E. 2003a. Herbivory, disease, recruitment limitation and the success of an alien tree species. Ecology 84: 1489–1505.

Siemann E. and Rogers W.E. 2003b. Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. Oecologia 135: 451–457.

Siemann E. and Rogers W.E. 2003c. Increased competitive ability of an invasive tree may be limited by an invasive beetle. Ecol. Appl. 13: 1503–1507.

Simms E.L. 1992. Costs of plant resistance to herbivory. In: Fritz R.S. and Simms E.L. (eds), Plant Resistance to Herbivores and Pathogens. University of Chicago Press, Chicago, pp. 392–425.

Stowe K.A., Marquis R.J., Hochwender C.G. and Simms E.L. 2000. The evolutionary ecology of tolerance to consumer damage. Annu. Rev. Ecol. Syst. 31: 565–595.

Strauss S.Y., Rudgers J.A., Lau J.A. and Irwin R.E. 2002. Direct and ecological costs of resistance to herbivory. Trends Ecol. Evol. 17: 278–285.

Strong D.R., Lawton J.H. and Southwood T.R.E. 1984. Insects on Plants. Harvard Press, Cambridge.

Tiffin P. and Inouye B.D. 2000. Measuring tolerance to herbivory: accuracy and precision of estimates made using natural versus imposed damage. Evolution 54: 1024–1029.

Tilman D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455–1474.

Ueckert D.N. and Hansen R.M. 1971. Dietary overlap of grasshoppers on sandhill rangeland in northeastern Colorado. Oecologia 8: 276–295.

van der Meijden E., Wijn M. and Verkaar H.J. 1988. Defence and regrowth, alternative strategies in the struggle against herbivores. Oikos 51: 355–363.

van Kleunen M. and Schmid B. 2003. No evidence for an evolutionary increased competitive ability in an invasive plant. Ecology 84: 2816–2823.

Weis A., Simms E.L. and Hochberg M. 2000. Will plant vigor and tolerance be genetically correlated? Effects of intrinsic growth rate and self-limitation on regrowth. Evol. Ecol. 14: 331–352.

Willis A.J., Thomas M. and Lawton J. 1999. Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? Oecologia 120: 632–640.

Yela J.L. and Lawton J.H. 1997. Insect herbivore loads on native and introduced plants: a preliminary study. Entomol. Exp. Appl. 85: 275–279.