Journal of Applied Ecology 2004 **41**, 561–570

Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*

WILLIAM E. ROGERS and EVAN SIEMANN

Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77005, USA

Summary

1. The evolution of increased competitive ability (EICA) hypothesis proposes that exotic plants often become invasive because they have evolved reduced allocation to defence and increased allocation to growth and reproduction in response to low herbivore loads. Previous studies with Chinese tallow tree *Sapium sebiferum* support EICA predictions of invasive North American ecotypes displaying rapid growth, poorly defended leaves and considerable compensation after defoliation. In contrast, native Asian ecotypes are comparatively slow growing with highly defended leaves and are negatively impacted by mechanical leaf damage. The effects of root damage on the different ecotypes are unknown.

2. We conducted a full-factorial pot experiment designed to assess the effects of soil fertility, competition with ryegrass *Lolium multiflorum* and mechanical root damage on *Sapium* seedlings derived from seed collections obtained in the ancestral range (native Chinese ecotype) and introduced range (invasive Texas ecotype).

3. The results, consistent with EICA predictions, revealed that Chinese ecotypes were negatively affected by severing roots, while Texas ecotypes were able to compensate for root damage.

4. Fertilization increased growth of Chinese ecotypes, but did not reduce the negative effects of root damage enough to allow the seedlings to compensate completely. Competition increased the stem height growth of Chinese ecotypes, but did not affect shoot or root mass. Texas ecotypes were not significantly affected by any experimental treatments.

5. *Synthesis and applications.* The results of this study are consistent with previous studies indicating that invasive *Sapium* has undergone a shift away from possessing costly herbivore defences to producing relatively inexpensive tissues that are capable of rapidly compensating for damage. Evolutionary change is increasingly being recognized as an important factor contributing to the success of exotic plant invaders. Understanding that herbivory tolerance and the compensatory capacity for damage may differ between native and introduced plant ecotypes will be essential for implementing effective control strategies for problematic invasive species.

Key-words: alien tree, compensatory growth, EICA hypothesis, tolerance, woody invader.

Journal of Applied Ecology (2004) 41, 561-570

Introduction

Deliberately introduced perennial woody species are frequently the most aggressive invaders of natural habitats and are an emerging threat to ecosystems

Correspondence: W. E. Rogers, Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77005, USA (fax +1 713 348 5232; e-mail wer@rice.edu). world-wide (Reichard & Hamilton 1997; Richardson 1998; Mack *et al.* 2000; Kriticos *et al.* 2003). Chinese tallow tree *Sapium sebiferum* (L.) Roxb. (Euphorbiaceae) is a serious invader in the south-eastern USA that aggressively displaces native plants and forms monotypic woodlands (Jubinsky & Anderson 1996; Bruce *et al.* 1997; Grace 1998). *Sapium* loses very small amounts of leaf area to herbivory in the USA (Scheld & Cowles 1981; Siemann & Rogers 2001, 2003a) and its advantage over

© 2004 British Ecological Society **562** W. E. Rogers & E. Siemann native plants is assumed to be partially due to a low pest load (Scheld & Cowles 1981; Jubinsky & Anderson 1996; Bruce *et al.* 1997). However, recent investigations have revealed that in addition to benefiting from an 'enemy release' (*sensu* Keane & Crawley 2002), *Sapium* has evolved a reduction in defence allocation and an increase in allocation to growth and/or reproduction in response to the absence of herbivores (Siemann & Rogers 2001, 2003b,c).

Formalized as the evolution of increased competitive ability (EICA) hypothesis (Blossey & Nötzold 1995), the role of evolutionary change in biological invasions is increasingly becoming recognized as a potentially important explanation for the success of alien invaders (Mack et al. 2000; Hänfling & Kollmann 2002; Lee 2002). The EICA hypothesis predicts that ecotypes from a plant's introduced range (invasive ecotypes) will be fast growing but more poorly defended against enemies than ecotypes from its ancestral range (native ecotypes). Because allocation to defence may be as costly as herbivore damage (Bazzaz et al. 1987; Simms 1992; Strauss et al. 2002), plants that escape their enemies in an introduced range should gain a selective benefit from decreasing their defensive investment. Foliar tissue analysis and mechanical damage studies using invasive and native ecotypes of Sapium are also consistent with the hypothesis that native ecotypes possess well-defended leaves that are costly to replace (Siemann & Rogers 2001; Rogers & Siemann 2004), whereas invasive ecotypes are capable of rapid compensatory growth following defoliation (Rogers et al. 2000; Rogers & Siemann 2002, 2003).

Root systems are typically better sheltered than aboveground plant parts and root herbivory is often less frequent, albeit more detrimental, than foliar herbivory (Reichman & Smith 1991; Strong et al. 1995; Maron 1998; but see Moran & Whitham 1990; Houle & Simard 1996). There has been considerably less attention paid to the role of subterranean herbivores than their aboveground, leaf-eating counterparts, despite the probable importance of root herbivory in plant population dynamics and in structuring terrestrial communities (Andersen 1987; Brown & Gange 1990; Mortimer, van der Putten & Brown 1999). Root tissues make attractive food sources for soil-dwelling herbivores. As a result, roots are often protected by chemical defences, especially in long-lived trees with low root : shoot ratios (Andersen 1987; Brown & Gange 1990).

Several root-feeding insects associated with *Sapium* have been identified in its native Asian range (Zhang & Lin 1994) but the effects of root damage on invasive North American ecotypes and its effect on plant competition have not been previously examined. To test the predictions of the EICA hypothesis with respect to *Sapium* root tissue, we conducted a full-factorial pot experiment designed to assess the effects of mechanical root damage, soil fertility and below-ground competition on the growth of *Sapium* seedlings derived from seeds obtained from the species' ancestral Chinese

range and introduced range along the Texas Gulf Coast. We chose to focus on early life-history stages because they are more likely to reveal mechanisms that regulate community dynamics (Fenner 1987; Meiners & Handel 2000; Howard & Goldberg 2001; Sheppard et al. 2002). Seedlings are frequently more susceptible to environmental stress than older plants and the effects of belowground herbivory are particularly severe in young plants with small root systems (Müller-Schärer 1991; Prins, Nell & Klinkhamer 1992; Strong et al. 1995). As a result, we predicted that (i) in accordance with the EICA hypothesis, growth of native Chinese ecotypes would be significantly reduced by root damage, whereas invasive Texas ecotypes that allocate resources to rapid regrowth would more fully compensate for the damage; (ii) additional soil nutrients would allow native ecotypes to partially compensate for tissue damage and would increase the growth of both ecotypes; and (iii) competition would reduce growth of tree seedlings subjected to root damage, although undamaged seedlings would escape competition and be unaffected by shallow rooting grass due to Sapium's taproot anatomy.

Materials and methods

STUDY SPECIES

Sapium sebiferum is a serious invader throughout the south-eastern USA. It is deciduous and has range limits largely determined by winter temperatures and aridity (Bruce *et al.* 1997). Rapid growth, colourful autumn foliage, abundant flowers and seeds rich in oils have encouraged extensive planting of *Sapium* (for detailed description of natural history see Siemann & Rogers 2003a). It regularly escapes cultivation and aggressively invades native ecosystems and displaces native plants (Jubinsky & Anderson 1996; Bruce *et al.* 1997; Grace 1998).

EXPERIMENTAL DESIGN

Seeds of both native and introduced Sapium trees were germinated in a glasshouse during April-May 2002. Native Chinese seeds were collected from a range of trees in the Guangdong province of China (Chinese ecotype and native ecotype used synonymously henceforth), while introduced seeds were collected from naturalized Sapium trees in Galveston County, Texas, USA (Texas ecotype and invasive ecotype used synonymously henceforth). The seeds were collected from many different trees within each region and grouped by continental origin. Seed weights did not differ statistically between the two ecotypes. Seeds and seedlings of the two ecotypes were visually indistinguishable except that Chinese ecotype seeds tended to germinate earlier than Texas ecotype seeds in the glasshouse (W.E. Rogers, personal observation). We germinated the seeds in single-celled, 100-mL ConetainersTM (Stuewe and Sons Inc., Corvallis, OR) filled with a homogenized mixture

of topsoil, organic humus and peat. Once the seedlings had primary leaves, they were placed beneath a 50% shade cloth outdoors for approximately 4 weeks.

To begin the experiment, we selected 48 Sapium seedlings of Chinese ecotypes and 48 Sapium seedlings of Texas ecotypes and individually transplanted them into 7.65-L TreepotsTM (Stuewe and Sons Inc.) filled with a 3:1 homogenized mixture of commercially available topsoil and fine-grained sand, respectively. The pots were placed in a temperature-controlled (27 °C) laboratory area. The northern exposure of the room was mostly windows that provided an average of 530 μ mol m⁻² s⁻¹ diffuse PAR during peak light, as measured by an ACCUPAR Ceptometer (Decagon Devices, Pullman, WA). Full-spectrum lights suspended over the pots provided an additional 85 μ mol m⁻² s⁻¹ PAR on a 12-h light-12-h dark cycle. A small oscillating fan was used to increase air circulation. In order to prevent fungal pathogen build-up, we twice sprayed mancozeb (DuPont Agricultural Products, Wilmington, DE) on the plants. Separate phytotoxicity tests have found no negative effects of this fungicide on Sapium (Siemann & Rogers 2003a). We watered the plants daily and turned the pots 180° in place twice per week and rotated them among positions within the experiment biweekly to minimize shading and location effects.

On 25 June 2002, we measured stem height on each seedling before initiating a 150-day experiment. Sapium seedlings were randomly assigned a mechanical root damage, nutrient addition or grass competition treatment to establish a full-factorial experimental design. Treatment combinations were replicated six times for each ecotype. Supplemental nutrients were added as 3 g m⁻² nitrogen (N), 1 g m⁻² phosphorus (P), 2 g m⁻² potassium (K) from a 15-5-10 NPK fertilizer per plot per application on 18 July and 13 September. Competition was initiated on 2 August by adding annual ryegrass seed Lolium multiflorum Lam. to the pots at the recommended rate of 50 g m⁻² (1.5 g pot⁻¹). Grass seeds were thinly covered with topsoil and began germinating within 2 days. On 5 September, herbivore damage was simulated by mechanically severing the entire root system 5 cm below the soil surface. Roots were severed using a sharp serrated steel blade inserted into a narrow opening cut in the plastic pot. Test pots were used prior to initiating root damage to ensure the effectiveness of this method. Realistic simulation of herbivory by mechanical means is problematic because many aspects of consumption cannot be duplicated accurately (Andersen 1987; Hendrix 1988; Baldwin 1990; Blossey & Hunt-Joshi 2003); however, mechanical damage offers some advantages over using herbivores and can provide a useful representation of tissue loss (Reichman & Smith 1991; Stowe et al. 2000; Tiffin & Inouye 2000). On 29 October, we took a final measurement of stem height. 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. Larger Sapium

© 2004 British Ecological Society, Journal of Applied Ecology, **41**, 561–570 roots were easily distinguished from *Lolium* roots and carefully separated. *Lolium* roots and very fine *Sapium* roots were not retained because it was not possible to separate them. Dead, severed *Sapium* root masses in mechanical damage treatments were also discarded. *Sapium* shoots and roots and *Lolium* shoots were dried at 60 °C for at least 65 h and weighed separately.

DATA ANALYSES

Stem growth was calculated as [ln(final mm/initial mm)], where initial height was measured on 25 June prior to initiation of the experimental treatments and final height was measured on 29 October prior to plant harvest. Competitive success was measured as the ratio of Sapium shoot mass/(Sapium shoot mass + Lolium shoot mass). We used a nested analysis of variance (ANOVA) to compare the measurements of stem growth and plant mass between the different experimental treatments (SAS Institute, Cary, NC). A nested analysis allows root damage to be examined as a function of Sapium ecotype, fertilization and competition. This controls for differences in plant size, root mass and rooting depth that may result from responses to these treatments prior to damaging the roots. A four-way factorial analysis is statistically robust, but it makes examination of the effects of experimental treatments on each ecotype difficult due to size differences between ecotypes that were sustained for the duration of the experiment. As a result, we also analysed each Sapium ecotype with separate three-way factorial analyses (sensu Shaver & Chapin 1980; Mitchell, Arthur & Farrow 1992). Mass data were square-root transformed to meet the statistical assumptions of ANOVA and back-transformed for presentation.

Results

Although several seedlings lost their leaves in the week after the mechanical root damage, all of the *Sapium* seedlings added new leaves and survived the 150-day experiment. The four-way nested ANOVA revealed that stem height growth ($F_{1,80} = 18.91$, P < 0.0001), shoot mass ($F_{1,80} = 42.58$, P < 0.0001) and root mass ($F_{1,80} = 24.43$, P < 0.0001) were all significantly different between Chinese and Texas ecotypes (Table 1). The Chinese ecotypes were initially larger than the Texas ecotypes and these size differences were sustained for the duration of the experiment (Table 2). Presumably, these differences were due to the earlier germination of Chinese ecotypes resulting in larger seedlings.

Additional soil nutrients increased the stem height growth ($F_{1,80} = 6 \cdot 1$, $P = 0 \cdot 02$), shoot mass ($F_{1,80} = 14 \cdot 74$, $P = 0 \cdot 0002$) and root mass ($F_{1,80} = 17 \cdot 93$, $P < 0 \cdot 0001$) of *Sapium* seedlings, but there were also significant interactions of nutrients with ecotype (stem growth: $F_{1,80} = 7 \cdot 82$, $P = 0 \cdot 006$; shoot mass: $F_{1,80} = 6 \cdot 83$, P = $0 \cdot 01$; root mass: $F_{1,80} = 3 \cdot 2$, $P = 0 \cdot 08$; Table 1), suggesting a differential response of the two ecotypes to **Table 1.** Four-way nested analyses of variance table of stem height growth [ln(final mm/initial mm)], square-root transformed shoot mass and square-root transformed root mass for *Sapium sebiferum* tree seedlings. Nested analyses allow root damage to be examined as a function of *Sapium* ecotype, NPK nutrient addition and competition with ryegrass. Experimental treatments: E, *Sapium* ecotype; N, NPK nutrient addition; C, grass competition; R, mechanical root damage. Msq, mean square

		Stem grov	wth	Shoot mass		Root mass	
	d.f.	Msq	<i>F</i> -value	Msq	<i>F</i> -value	Msq	F-value
Ecotype (E)	1	1.699	18.91****	1.805	42.58****	0.409	24.43****
Nutrients (N)	1	0.548	6.10*	0.625	14.74***	0.300	17.93****
Competition (C)	1	0.597	6.64*	0.010	0·24 NS	0.019	1·12 NS
E×N	1	0.703	7.82**	0.290	6.83**	0.054	3.20†
$E \times C$	1	0.016	0.18 NS	0.011	0.25 NS	0.002	0.14 NS
$N \times C$	1	0.009	0.10 NS	0.003	0.07 NS	0.028	1.67 NS
$E \times N \times C$	1	0.126	1.40 NS	0.142	3.35†	0.040	2·42 NS
$R(E \times N \times C)$	8	0.192	2.14*	0.072	1.71†	0.040	2.40*
Error	80	0.090		0.042			

P-value: NS, not significant; $\dagger \le 0.1$; $\ast \le 0.05$; $\ast \ast \le 0.01$; $\ast \ast \ast \le 0.001$; $\ast \ast \ast \ast \le 0.0001$.

additional nutrients (see below). Sapium height growth was also significantly increased by below-ground competition ($F_{1.80} = 6.64$, P = 0.01; Table 1). The most informative results provided by the nested four-way ANOVA model were the significant effects of mechanical root damage as a function of Sapium ecotype, nutrient addition and competition on these growth parameters (Table 1). Stem height growth ($F_{8.80} = 2.14$, P =0.04), shoot mass ($F_{8,80} = 1.71$, P = 0.1) and root mass $(F_{8,80} = 2.4, P = 0.02)$ of *Sapium* seedlings were differentially affected by mechanical root damage as a function of continental origin, soil fertility and competitive environment. These results suggested that Chinese and Texas ecotypes grown under various fertility and competitive conditions are differentially responding to mechanical root damage. Separate three-way factorial analyses provided greater insights into the magnitude of the responses of Chinese and Texas ecotypes to root damage, fertility and competition.

The three-way ANOVA model revealed that *Sapium* growth in stem height for Chinese ecotype seedlings was significantly affected by the main effects of all three experimental treatments (Table 2a). Stem height growth of Chinese ecotypes was negatively affected by root damage ($F_{1,40} = 13.08$, P = 0.0008) but positively affected by fertilization ($F_{1,40} = 13.56$, P = 0.0007) and grass competition ($F_{1,40} = 4.394$, P = 0.04; Table 3a). Stem height growth of Texas ecotypes was not significantly affected by any experimental treatments (Tables 2b and 3b).

Sapium shoot mass for Chinese ecotypes was significantly decreased by mechanical root damage ($F_{1,40} = 8.165$, P = 0.007) and increased by fertilization ($F_{1,40} = 17.81$, P = 0.0001; Tables 2a and 3a). Similarly, root mass for Chinese ecotypes was significantly decreased by mechanical root damage ($F_{1,40} = 10.27$, P = 0.003; Tables 2a and 3a) and increased by fertilization ($F_{1,40} = 22.1$, $P \le 0.0001$; Tables 2a and 3a). Shoot mass and root mass of Texas ecotypes were not significantly affected by root damage, fertilization or competition

(Tables 2b and 3b). The percentage of damaged Sapium mass relative to undamaged plants receiving the same fertilizer treatment highlighted the differential response of Chinese and Texas ecotypes seedlings in competitive conditions (Fig. 1a,b). Shoot and root mass of Chinese ecotypes were markedly reduced by mechanical root damage in both fertilized and unfertilized conditions (Fig. 1a), whereas both shoot and root mass of Texas ecotypes showed high compensatory capacities for root damage, particularly with increased fertility (Fig. 1b). Further, Sapium competitive success was significantly reduced by root damage in pots containing Chinese ecotypes ($F_{1,20} = 4.343$, P = 0.05; Table 4a and Fig. 2a) while the competitive success of Texas ecotypes was not significantly affected by any experimental treatments (Table 4b and Fig. 2b).

In competition pots, *Lolium* shoot mass was significantly increased by fertilization in both pots containing Chinese ($F_{1,20} = 30.39$, P < 0.0001; Table 4a) and Texas ($F_{1,20} = 16.47$, P = 0.0006; Table 4b) ecotypes. A significant interaction between mechanical root damage and fertilization also occurred for *Lolium* shoot mass in pots containing Texas ecotypes ($F_{1,20} = 14.3$, P = 0.001), with the least mass in unfertilized pots with damage and the most mass in unfertilized pots without damage (Table 4b).

Discussion

Ecological theory predicts that a trade-off exists between herbivory tolerance (i.e. mechanisms that facilitate regrowth following tissue damage) and herbivory resistance (i.e. mechanisms that reduce the probability of consumption) (van der Meijden, Wijn & Verkaar 1988; Herms & Mattson 1992; Simms 1992; Fineblum & Rausher 1995; Mauricio 2000; Pilson 2000; Strauss *et al.* 2002). Resistant plants invest resources and energy into producing and maintaining defences, while tolerant plants rapidly regrow following tissue loss. The EICA hypothesis suggests that, in response to low pest loads,

	No added nutrien	ts			NPK added				
1	Vo competition		Grass present		No competition		Grass present		
	Vo damage	Root damage	No damage	Root damage	No damage	Root damage	No damage	Root damage	ANOVA
(a) Chinese									
Stem growth	0.287 + 0.14	0.080 + 0.15	0.653 + 0.05	0.265 ± 0.14	0.783 + 0.09	0.413 + 0.14	0.840 + 0.14	0.539 + 0.11	R, N, C
Shoot mass	0.321 + 0.08	0.236 + 0.08	0.442 + 0.06	0.318 + 0.08	1.055 + 0.20	0.555 + 0.18	0.869 + 0.27	0.440 + 0.14	R, N
Root mass	0.278 + 0.05	0.224 + 0.04	0.238 + 0.03	0.203 + 0.03	0.578 + 0.07	0.326 + 0.06	0.486 + 0.13	0.297 + 0.04	R, N
(b) Texas									
Stem growth	0.239 + 0.11	0.135 + 0.11	0.366 + 0.10	0.166 + 0.10	0.195 + 0.12	0.033 + 0.16	0.360 + 0.13	0.238 + 0.12	All NS
Shoot mass	0.217 + 0.10	0.137 + 0.05	0.161 + 0.02	0.151 + 0.06	0.205 + 0.08	0.126 + 0.04	0.226 + 0.07	0.298 + 0.14	All NS
Root mass	0.246 + 0.04	0.159 + 0.05	0.133 + 0.02	0.118 + 0.03	0.280 + 0.08	0.119 + 0.03	0.239 + 0.09	0.249 + 0.07	All NS

Table 2. Means (+ 1 SE) and analysis of variance (avova) for growth parameters of (a) native Chinese and (b) invasive Texas Sapium seedlings planted in pots in a full-factorial experimental design with NPK

many introduced plants become invasive by evolving increased rates of growth and reproduction while concurrently reducing costly herbivore deterrents (Blossey & Nötzold 1995). Our results are consistent with the predictions of the EICA hypothesis. *Sapium* height growth, shoot mass, root mass and competitive ability of native Chinese ecotypes were all significantly reduced by mechanically severed roots, whereas invasive Texas ecotypes better compensated for damage.

Simulated herbivory studies have been criticized because artificial damage often removes more tissue than herbivores in natural conditions and exaggerates damage severity (Hendrix 1988; Baldwin 1990). However, this concern strengthens support for the EICA hypothesis in our study because Texas ecotypes compensated for these high damage levels over a relatively short time period. Long-lived perennial plants often replace tissues lost to herbivory damage over several growing seasons (Hendrix 1988; Sacchi & Conner 1999; Haukioja & Koricheva 2000) suggesting that Chinese ecotypes may compensate for damage with time. Regardless, it is the differential responses of the native vs. invasive ecotypes to tolerate and compensate for root damage in the short term that most strongly emphasizes their evolutionary divergence.

The ability of a plant to compensate for tissue damage can be strongly influenced by soil resources. Negative effects of root damage can be particularly pronounced with low nutrient availability and are expected to be mitigated by an increased supply of limiting resources (Maschinski & Whitham 1989; Brown & Gange 1990; Steinger & Müller-Schärer 1992; Verschoor et al. 2002). Also, increased soil fertility can potentially offset the cost of producing energetically expensive secondary metabolites contained in many roots (Andersen 1987; Brown & Gange 1989; Mortimer, van der Putten & Brown 1999). However, results from root damage studies are inconsistent. Soil fertility greatly influenced the capacity of Centaurea to compensate for root damage (Steinger & Müller-Schärer 1992), but did not ameliorate negative effects of below-ground herbivory in Solidago (Schmid, Miao & Bazzaz 1990), Salix (Houle & Simard 1996), Holcus or Anthoxanthum (Verschoor et al. 2002). In our study, additional soil nutrients increased height growth and mass of native Chinese ecotypes, but there was no significant interaction between nutrient addition and root damage. Thus, it does not appear that additional soil resources were able to increase the compensatory capacity of Chinese ecotypes, thereby reducing the negative effects of mechanically severed roots.

Below-ground herbivory can have strong effects on plant community structure and the competitive environment of a plant often influences its response to root damage (Andersen 1987; Brown & Gange 1990; Mortimer, van der Putten & Brown 1999; Rogers & Hartnett 2001; Verschoor *et al.* 2002). Several studies have found the impact of below-ground herbivory to be greater when the host-plant was competing with other

Table 3. Three-way analyses of variance tables of stem height growth [ln(final mm/initial mm)], square-root transformed shoot mass and square-root transformed root mass for *Sapium sebiferum* tree seedlings derived from (a) Chinese and (b) Texas seed in response to the experimental treatments: R, mechanical root damage; N, NPK nutrient addition; C, grass competition. Msq, mean square

		Stem grow	th	Shoot mas	S	Root mass	
	d.f.	Msq	<i>F</i> -value	Msq	<i>F</i> -value	Msq	<i>F</i> -value
(a) Chinese ecotype							
Root damage (R)	1	1.202	13.08 ***	0.405	8.165 **	0.141	10.27 **
Nutrients (N)	1	1.246	13.56 ***	0.883	17.81 ****	0.303	22.10 ****
Competition (C)	1	0.404	4.394 *	< 0.001	< 0.001 NS	0.017	1·254 NS
$\mathbf{R} \times \mathbf{N}$	1	0.004	0.048 NS	0.102	2·067 NS	0.047	3·395 NS
$R \times C$	1	0.009	0.099 NS	< 0.001	0.001 NS	0.002	0·153 NS
$N \times C$	1	0.102	1·108 NS	0.094	1.895 NS	0.001	0.042 NS
$R \times N \times C$	1	0.047	0.512 NS	0.001	0.018 NS	< 0.001	0.024 NS
Error	40	0.092		0.050		0.014	
(b) Texas ecotype							
Root damage (R)	1	0.260	2·961 NS	0.014	0·386 NS	0.064	3·234 NS
Nutrients (N)	1	0.005	0.055 NS	0.032	0.903 NS	0.020	2·534 NS
Competition (C)	1	0.209	2·379 NS	0.021	0·591 NS	0.004	0·196 NS
$\mathbf{R} \times \mathbf{N}$	1	< 0.001	0.003 NS	0.005	0·141 NS	0.002	0·122 NS
$R \times C$	1	0.002	0.028 NS	0.047	1·332 NS	0.055	2·773 NS
$N \times C$	1	0.033	0.380 NS	0.051	1.460 NS	0.068	3·439 NS
$R \times N \times C$	1	0.014	0·159 NS	0.005	0·155 NS	0.010	0.524 NS
Error	40	0.088		0.035		0.020	

P-value: NS, not significant; *≤ 0.05; **≤ 0.01; ***≤ 0.001; ****≤ 0.0001.



Fig. 1. Percentage *Sapium* shoot and root mass (means + 1 SE) of mechanically root damaged (a) Chinese and (b) Texas ecotype seedlings relative to undamaged control seedlings (100%) receiving the same fertilizer treatment and grown with grass competition (see Table 2).

Table 4. Two-way analyses of variance tables for square-root transformed *Lolium multiflorum* shoot mass and *Sapium* competitive success, square-root (*Sapium* shoot mass/[*Sapium* + *Lolium* shoot masses]), in pots containing seedlings derived from (a) Chinese and (b) Texas seed in response to experimental treatments: R, mechanical root damage; N, NPK nutrient addition

		Lolium shoo	ot mass	Competitive su	ccess
	d.f.	Msq	<i>F</i> -value	Msq	<i>F</i> -value
(a) Chinese ecotype					
Root damage (R)	1	0.018	1·456 NS	0.055	4.343*
Nutrients (N)	1	0.385	30.39****	0.004	0·286 NS
R×N	1	0.015	1·222 NS	0.008	0.595 NS
Error	20	0.013		0.013	
(b) Texas ecotype					
Root damage (R)	1	0.019	1.651 NS	0.003	0·276 NS
Nutrients (N)	1	0.191	16.47***	0.007	0.646 NS
R×N	1	0.166	14.30**	< 0.001	0.004 NS
Error	20	0.012		0.010	

P-value: NS, not significant; *≤ 0.05; **≤ 0.01; ***≤ 0.001; ****≤ 0.0001.



Fig. 2. Sapium competitive success (means + 1 SE) of (a) Chinese ecotype and (b) Texas ecotype seedlings in response to mechanical root damage and fertilization (see Table 4). Competitive success was calculated as *Sapium* shoot mass/(*Sapium* shoot mass + grass shoot mass) and standardized by the unfertilized, undamaged control for each ecotype.

© 2004 British Ecological Society, *Journal of Applied Ecology*, **41**, 561–570 plant species (Müller-Schärer 1991; Nötzold, Blossey & Newton 1998). We predicted below-ground competition would reduce growth of *Sapium* seedlings subjected to mechanical root damage, but would have no effect on undamaged seedlings due to the tree's taproot anatomy. Unexpectedly, competition increased shoot growth of Chinese ecotypes, but there was no corresponding increase in shoot mass. This response cannot be ascribed to etiolation because the seedlings were never shaded by the short-stature ryegrass. There were no significant interactions of root damage and competition for growth or mass of Chinese ecotypes, although 568 W. E. Rogers & E. Siemann root damage did significantly reduce the competitive success of Chinese ecotypes. Competition had no significant effect on any measure of growth of Texas ecotypes.

Above- and below-ground herbivores often damage plants simultaneously, and complex interactions between different types of tissue damage frequently become manifest in varied growth responses (Seastedt, Ramundo & Hayes 1988; Moran & Whitham 1990; Houle & Simard 1996; Maron 1998; Masters, Jones & Rogers 2001). Other studies have shown that root herbivory has a greater negative effect on plant growth and reproduction than foliar herbivory (Reichman & Smith 1991; Strong et al. 1995; Maron 1998; but see Moran & Whitham 1990; Houle & Simard 1996). Simulated herbivory on the taprooted perennial Tragopogon dubius revealed significantly greater negative effects of damage to root tissues compared with equivalent losses of leaf tissue (Reichman & Smith 1991). Defoliation experiments with Sapium show similar growth reductions in Chinese ecotypes and compensatory ability in Texas ecotypes to the root damage responses reported here (Rogers & Siemann 2004). Future studies that jointly damage Sapium roots and shoots will provide important insights into both the level of tolerance in Texas ecotypes and the magnitude of damage susceptibility in Chinese ecotypes.

The most notable result of this study is that Texas ecotypes were not significantly affected by mechanical root damage relative to undamaged plants, whereas all aspects of growth for Chinese ecotypes were negatively impacted by root damage, compared with undamaged plants. These results are consistent with our other studies revealing that invasive North American ecotypes of Sapium are capable of considerable herbivory tolerance and rapid compensatory regrowth (Rogers et al. 2000; Rogers & Siemann 2002, 2003), whereas native Asian ecotypes of Sapium allocate significantly greater resources to costly defences (Siemann & Rogers 2001, 2003b, c) and leaf damage results in significantly reduced growth (Rogers & Siemann 2004). While these previous studies have focused primarily on the role of leaf chemistry and folivory, the present experiment examines the EICA hypothesis from the perspective of mechanical root damage and provides new, corroborative insights into the equivalent importance of below-ground tissues.

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 probably had more root mass removed. We do not believe this accounts for our findings accurately. A similar argument could claim that if Texas ecotypes were larger than Chinese ecotypes, the larger seedlings were better able to compensate for losses to herbivory. Several lines of research suggest that woody tree seedlings are most vulnerable when they are small during early life-history stages (Fenner 1987; Meiners & Handel 2000). As a result, we maintain that in a relatively brief period of time *Sapium* has evolved from a herbivore-resistant tree into an herbivore-tolerant

© 2004 British Ecological Society, *Journal of Applied Ecology*, **41**, 561–570 tree that rapidly compensates for tissue damage in a variety of resource conditions.

The considerable herbivory tolerance and compensatory capacity we have demonstrated for invasive Sapium ecotypes in this and other studies (Siemann & Rogers 2001, 2003b,c; Rogers & Siemann 2002, 2003) will better inform control efforts to eradicate this aggressive alien tree. Land managers view Chinese tallow tree as an excellent candidate for biological control because it is taxonomically isolated in the south-eastern USA (McFayden 1998; Pemberton 2000). There are certain advantages to using introduced root herbivores alone or in conjunction with folivores as biological control agents for other invasive plants in North America (Müller-Schärer 1991; Prins, Nell & Klinkhamer 1992; Blossey 1993; McEvoy & Coombs 1993; Blossey & Hunt-Joshi 2003), but similar efforts for Sapium should proceed with the knowledge that genetic differences in herbivore tolerance of native and invasive Sapium ecotypes may significantly modify the effectiveness of its native pests. Evolutionary change is increasingly being recognized as an important factor contributing to the success of exotic invaders. Understanding that the compensatory capacity for herbivore damage may differ between native and introduced plant ecotypes will be essential for implementing effective biological control strategies for problematic invasive species.

Acknowledgements

We would like to thank Brad Butterfield, Maria Hartley, Victoria Keener, Rick Lankau, and Daniel Mee for assistance, Yao Huang, Xang Yanci and Jie Lin for assistance in obtaining seeds from China, and the University of Houston Coastal Center for permission to collect Texas seeds. Support for this research was provided by the US National Science Foundation (DEB-9981654).

References

- Andersen, D.C. (1987) Below-ground herbivory in natural communities: a review emphasizing fossorial animals. *Quarterly Review of Biology*, **62**, 261–286.
- Baldwin, I.T. (1990) Herbivory simulations in ecological research. *Trends in Ecology and Evolution*, **5**, 91–93.
- Bazzaz, F.A., Chiariello, N.R., Coley, P.D. & Pitelka, L.F. (1987) Allocating resources to reproduction and defense. *Bioscience*, 37, 58–67.
- Blossey, B. (1993) Herbivory below ground and biological weed control: life history of a root-boring weevil on purple loosestrife. *Oecologia*, **94**, 80–387.
- Blossey, B. & Hunt-Joshi, T.R. (2003) Belowground herbivory by insects: influence on plants and aboveground herbivores. *Annual Review of Entomology*, 48, 521–547.
- Blossey, B. & Nötzold, R. (1995) Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *Journal of Ecology*, 83, 887–889.
- Brown, V.K. & Gange, A.C. (1990) Insect herbivory below ground. Advances in Ecological Research, 20, 1–58.
- Bruce, K.A., Cameron, G.N., Harcombe, P.A. & Jubinsky, G. (1997) Introduction, impact on native habitats, and

management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. *Natural Areas Journal*, **17**, 255–260.

- Fenner, M. (1987) Seedlings. Canadian Journal of Botany, 106, 35–47.
- Fineblum, W.L. & Rausher, M.D. (1995) Tradeoff between resistance and tolerance to herbivore damage in a morning glory. *Nature*, 377, 517–520.
- Grace, J.B. (1998) Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? *Endangered Species Update*, **15**, 70–76.
- Hänfling, B. & Kollmann, J. (2002) An evolutionary perspective of biological invasions. *Trends in Ecology and Evolution*, 17, 545–546.
- Haukioja, E. & Koricheva, J. (2000) Tolerance to herbivory in woody vs. herbaceous plants. *Evolutionary Ecology*, 14, 551–562.
- Hendrix, S.D. (1988) Herbivory and its impact on plant reproduction. *Plant Reproductive Ecology: Patterns and Strategies* (eds J. Lovett-Doust & L. Lovett-Doust), pp. 246–263. Oxford University Press, New York, NY.
- Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants: to grow or to defend. *Quarterly Review of Biology*, 67, 283–335.
- Houle, G. & Simard, G. (1996) Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory response of *Salix planifolia* ssp. *planifolia* to simulated herbivory. *Oecologia*, **107**, 373–378.
- Howard, T.G. & Goldberg, D.E. (2001) Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology*, **82**, 979–990.
- Jubinsky, G. & Anderson, L.C. (1996) The invasive potential of Chinese tallow-tree (*Sapium sebiferum* Roxb.) in the southeast. *Castanea*, **61**, 226–231.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.
- Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.W. & Maywald, G.F. (2003) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *Journal of Applied Ecology*, **40**, 111– 124.
- Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*, **17**, 386–391.
- McEvoy, P.B. & Coombs, E.M. (1993) Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications*, 9, 387–401.
- McFayden, R.E. (1998) Biological control of weeds. Annual Review of Entomology, 43, 369–393.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Maron, J.L. (1998) Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology*, 79, 1281–1293.
- Maschinski, J. & Whitham, T. (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. *American Naturalist*, **134**, 1–19.
- Masters, G.J., Jones, T.H. & Rogers, M. (2001) Host-plant mediated effects of root herbivory on insect seed predators and their parasitoids. *Oecologia*, **127**, 246–250.
- Mauricio, R. (2000) Natural selection and the joint evolution of tolerance and resistance as plant defenses. *Evolutionary Ecology*, 14, 491–507.

© 2004 British Ecological Society, *Journal of Applied Ecology*, **41**, 561–570

- van der Meijden, E., Wijn, M. & Verkaar, H.J. (1988) Defence and regrowth, alternative strategies in the struggle against herbivores. *Oikos*, **51**, 355–363.
- Meiners, S.J. & Handel, S.N. (2000) Additive and nonadditive effects of herbivory and competition on tree seedling

mortality, growth, and allocation. *American Journal of Botany*, **87**, 1821–1826.

- Mitchell, P., Arthur, W. & Farrow, M. (1992) An investigation of population limitation using factorial experiments. *Ecology*, 61, 591–598.
- Moran, N.A. & Whitham, T.G. (1990) Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. *Ecology*, **71**, 1050–1058.
- Mortimer, S.R., Van der Putten, W.H. & Brown, V.K. (1999) Insect and nematode herbivory below ground: interactions and role in vegetation succession. *Herbivores: Between Plants and Predators* (eds H. Olff, V.K. Brown & R.H. Drent), pp. 205–238. Blackwell Science, Oxford.
- Müller-Schärer, H. (1991) The impact of root herbivory as a function of plant density and competition: survival, growth and fecundity of *Centaurea maculosa* in field plots. *Journal* of *Applied Ecology*, 28, 759–776.
- Nötzold, R., Blossey, B. & Newton, E. (1998) The influence of below ground herbivory and plant competition on growth and biomass of purple loosestrife. *Oecologia*, **113**, 82–93.
- Pemberton, R.W. (2000) Predictable risk to native plants in weed biological control. *Oecologia*, **125**, 489–494.
- Pilson, D. (2000) The evolution of plant response to herbivory: simultaneously considering resistance and tolerance in *Brassica rapa*. *Evolutionary Ecology*, **14**, 457–489.
- Prins, A.H., Nell, H.W. & Klinkhamer, P.G.L. (1992) Sizedependent root herbivory on *Cynoglossum officinale*. Oikos, 65, 409–413.
- Reichard, S.H. & Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Conser*vation Biology, 11, 193–203.
- Reichman, O.J. & Smith, C.C. (1991) Responses to simulated leaf and root herbivory by a biennial, *Tragopogon dubius*. *Ecology*, **72**, 116–124.
- Richardson, D.M. (1998) Forestry trees as invasive aliens. Conservation Biology, 12, 18–26.
- Rogers, W.E. & Hartnett, D.C. (2001) Vegetation responses to different spatial patterns of soil disturbance in burned and unburned tallgrass prairie. *Plant Ecology*, **155**, 99–109.
- Rogers, W.E., Nijjer, S., Smith, C.L. & Siemann, E. (2000) Effects of resources and herbivory on leaf morphology and physiology of Chinese tallow (*Sapium sebiferum*) tree seedlings. *Texas Journal of Science*, **52S**, 43–56.
- Rogers, W.E. & Siemann, E. (2002) Effects of simulated herbivory and resource availability on native and invasive exotic tree seedlings. *Basic and Applied Ecology*, 3, 297–307.
- Rogers, W.E. & Siemann, E. (2003) Effects of simulated herbivory and resources on Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasion of native coastal prairie. *American Journal of Botany*, **90**, 243–249.
- Rogers, W.E. & Siemann, E. (2004) The role of herbivores in exotic plant invasions: insights using a combination of methods to enhance or reduce herbivory. *Insects and Ecosystem Function* (eds E. Siemann & W.W. Weisser), pp. 225– 276. Springer-Verlag, Berlin, Germany.
- Sacchi, C. & Conner, E. (1999) Changes in reproduction and architecture in flowering dogwood, *Cornus florida*, after attack by the dogwood club gall *Resseliella*. *Oikos*, 86, 138–146.
- Scheld, H.W. & Cowles, J.R. (1981) Woody biomass potential of the Chinese tallow tree. *Economic Botany*, 35, 391–397.
- Schmid, B., Miao, S.L. & Bazazz, F.A. (1990) Effects of simulated root herbivory and fertilizer application on growth and biomass allocation in the clonal perennial *Solidago canadensis*. *Oecologia*, 84, 9–15.
- Seastedt, T.R., Ramundo, R.A. & Hayes, D. (1988) Maximization of densities of soil animals by foliage herbivory: empirical evidence, graphical, conceptual models. *Oikos*, 51, 243–248.
- Shaver, G.R. & Chapin, F.S. (1980) Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. *Ecology*, **61**, 662–675.

569

570 W. E. Rogers & E. Siemann

- Sheppard, A.W., Hodge, P., Paynter, Q. & Rees, M. (2002) Factors affecting invasion and persistence of broom *Cytisus* scoparium in Australia. Journal of Applied Ecology, **39**, 721–734.
- Siemann, E. & Rogers, W.E. (2001) Genetic differences in growth of an invasive tree species. *Ecology Letters*, 4, 514–518.
- Siemann, E. & Rogers, W.E. (2003a) Herbivory, disease, recruitment limitation and success of alien and native tree species. *Ecology*, 84, 1489–1505.
- Siemann, E. & 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. & Rogers, W.E. (2003c) Increased competitive ability of an invasive tree may be limited by an invasive beetle. *Ecological Applications*, **13**, 1503–1507.
- Simms, E.L. (1992) Costs of plant resistance to herbivory. *Plant Resistance to Herbivores and Pathogens* (eds R. Fritz & E. Simms), pp. 392–425. University of Chicago Press, Chicago, IL.
- Steinger, T. & Müller-Schärer, H. (1992) Physiological and growth responses of *Centaurea maculosa* (Asteraceae) to root herbivory under varying levels of interspecific plant competition and soil nitrogen availability. *Oecologia*, **91**, 141–149.

- Stowe, K., Marquis, R., Hochwender, C. & Simms, E. (2000) The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology and Systematics*, 31, 565–595.
- Strauss, S.Y., Rudgers, J.A., Lau, J.A. & Irwin, R.E. (2002) Direct and ecological costs of resistance to herbivory. *Trends in Ecology and Evolution*, 17, 278–285.
- Strong, D.R., Maron, J.L., Connors, P.G., Whipple, A., Harrison, S. & Jefferies, R.L. (1995) High mortality, fluctuation in numbers, and heavy subterranean insect herbivory in bush lupine, *Lupinus arboreus*. *Oecologia*, **104**, 85–92.
- Tiffin, P. & Inouye, B.D. (2000) Measuring tolerance to herbivory: accuracy and precision of estimates made using natural versus imposed damage. *Evolution*, 54, 1024–1029.
- Verschoor, B.C., Pronk, T.E., de Goede, R.G.M. & Brussaard, L. (2002) Could plant-feeding nematodes affect the competition between grass species during succession in grasslands under restoration management? *Journal of Ecology*, **90**, 753–761.
- Zhang, K. & Lin, Y. (1994) *Chinese Tallow*. China Forestry Press, Beijing, China.

Received 31 December 2002; final copy received 11 February 2004