

## Genetic differences in growth of an invasive tree species

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### Abstract

Invasive plants are often more vigorous in their introduced ranges than in their native ranges. This may reflect an innate superiority of plants from some habitats or an escape from their enemies. Another hypothesis proposes that invasive plants evolve increased competitive ability in their introduced range. We present the results of a 14-year common garden experiment with the Chinese Tallow Tree (*Sapium sebiferum*) from its native range (Asia), place of introduction to North America (Georgia) and areas colonized a century later (Louisiana and Texas). Invasive genotypes, especially those from recently colonized areas, were larger than native genotypes and more likely to produce seeds but had lower quality, poorly defended leaves. Our results demonstrate significant post-invasion genetic differences in an invasive plant species. Post-introduction adaptation by introduced plants may contribute to their invasive success and make it difficult to predict problem species.

### Keywords

Evolution of increased competitive ability, *Sapium sebiferum*, Chinese Tallow Tree, trade-off, invasion, plant growth, defence.

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### INTRODUCTION

Two factors are widely believed to increase the abundance and vigour of many invasive plants in their introduced range compared to their native range (Elton 1958; Blossey & Notzold 1995; Crawley 1987; Mack *et al.* 2000; Thebaud & Simberloff 2001). First, some species may be innately better competitors because they evolved in a more competitive environment (Darwin 1859; Crawley 1987; Vitousek & Walker 1989; Lodge 1993; Lonsdale 1999; Tilman 1999; Callaway & Aschehoug 2000; Davis *et al.* 2000). In their introduced range, invasive plants may compete only with competitively inferior plants, whereas in their native range they enjoy no such systematic advantage. Second, invasive plants frequently have low losses to enemies, particularly herbivores, in their introduced range (Elton 1958; Lodge 1993; Yela & Lawton 1997; Tilman 1999). In this benign environment, the resources normally lost to enemies may be allocated to growth and/or reproduction by a plastic phenotypic response (Bazzaz *et al.* 1987; Tilman 1999; Thebaud & Simberloff 2001).

An alternative hypothesis (Evolution of Increased Competitive Ability, 'EICA'; Blossey & Notzold 1995) proposes that invasive plants are seldom attacked by enemies in their

introduced range so they evolve reduced allocation to defence and increased allocation to growth and/or reproduction (Blossey & Notzold 1995; Daehler & Strong 1997; Willis *et al.* 1999, 2000; Thebaud & Simberloff 2001). Allocation to defence may be as costly as herbivore damage (Bazzaz *et al.* 1987; Simms & Rausher 1987; Baldwin *et al.* 1990). Only the EICA hypothesis predicts that genotypes from a plant's introduced range ('invasive genotypes') will grow faster and/or produce more seeds but be less well defended against enemies than genotypes from its native range ('native genotypes') if both are grown in a common environment. Greenhouse experiments have provided some evidence of evolution of decreased herbivore resistance in invasive plants (Daehler & Strong 1997). Field experiments have been encouraging but inconclusive (Blossey & Notzold 1995; Willis *et al.* 1999). They have sometimes shown genetic differences in growth of native and invasive genotypes (Blossey & Notzold 1995) but have also shown negative results (Willis *et al.* 2000; Thebaud & Simberloff 2001). No study has shown ecologically significant evolutionary increases in growth and/or reproduction and corresponding decreases in defence by an invasive plant in its introduced range (Mack *et al.* 2000; Mooney & Cleland 2001; Thebaud & Simberloff 2001).

## METHODS

### Focal species

In many areas of the south-eastern United States, the introduced Chinese Tallow Tree (*Sapium sebiferum* (L.) Roxb., Euphorbiaceae) aggressively displaces native plants and forms monospecific stands (Bruce *et al.* 1997). *Sapium* is native to Asia, where it is both naturally occurring and cultivated for 14 centuries (Bruce *et al.* 1997). *Sapium* was deliberately introduced to Georgia in the late 18th century from Asia for agricultural purposes and later to Texas and Louisiana by the United States government in the early 20th century (Bruce *et al.* 1997). The introductions to Texas and Louisiana were performed by the Bureau of Plant Industry before they began keeping systematic records of the sources of plant materials.

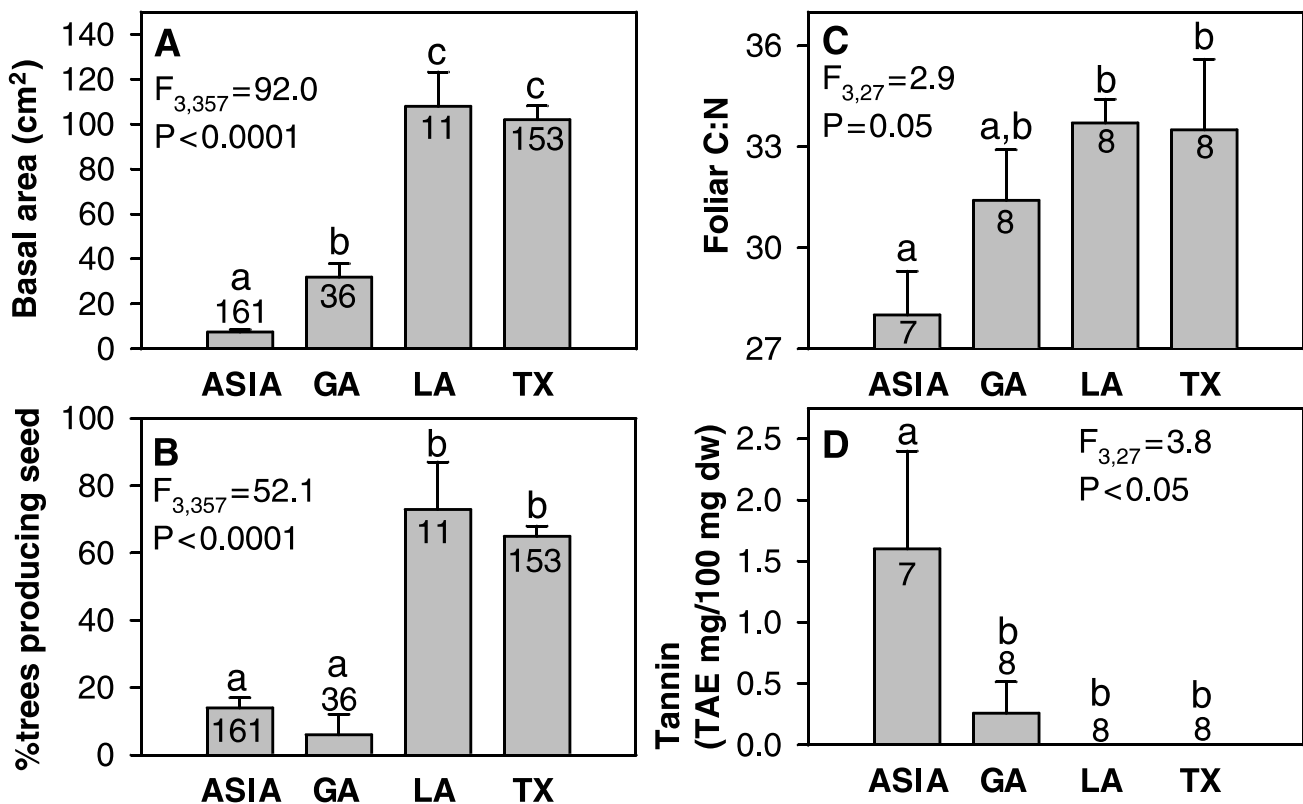
### Experimental design

In 1986, E. Glumac rototilled and planted a field in Galveston County, Texas, with *Sapium sebiferum* seedlings.

These were grown in a greenhouse using seeds collected from trees in Asia (14 source trees in Taiwan representing a range of locations and elevations), Georgia (three source trees), Louisiana (one source tree) and Texas (14 source trees). The original experimental design was randomized with 16 trees from each source tree and one tree per 1.5 m<sup>2</sup>. Two rows of border trees were planted to limit edge effects. In years 1–3, aisles were rototilled and the experiment was fertilized with 8 g/m<sup>2</sup> N, 8 g/m<sup>2</sup> P and 3 g/m<sup>2</sup> K. In the 8th year, Galveston County removed some trees from one end of the experiment, leaving an average of 11 trees (range 8–12) per source tree after designating the two outermost rows as the new border trees. No data were collected from the 6th to 13th years.

### Measurements in the 14th year

We measured diameter at breast height (d.b.h. – 137 cm) for all living stems of each tree. From this we calculated basal area for each tree. We visually determined whether each tree was producing seed. We collected leaves from



**Figure 1** Genotypes of *Sapium sebiferum* differed in (A) size, (B) seed production, (C) leaf chemistry, and (D) defence chemicals. Asia (native genotypes), GA = Georgia (site of North American introduction), LA = Louisiana, TX = Texas (areas colonized later). Bars are means  $\pm$  1 SE.  $F$ -values and  $P$ -values from ANOVAs. Different letters indicate means that were significantly different in Fisher's LSD means contrasts. Numbers indicate the number of trees sampled from that region.

eight randomly selected trees from each of the four geographical regions. We scanned 20 leaves of each tree on a flatbed scanner and measured average percent leaf area removed by chewing insects using the computer program NIH Image v.1.62 (<http://rsb.info.nih.gov/nih-image/>). Leaves were dried, ground, analysed for total carbon and nitrogen with an autoanalyser and assayed for tannin content using the radial diffusion protein precipitation method (Hagerman 1987) with a tannic acid standard. Tannin concentrations were expressed as the amount of tannic acid standard needed to precipitate the same amount of protein (TAE, Tannic Acid Equivalents) on a per dry weight (dw) leaf mass basis. One set of Asia leaves was lost in the grinding process. We used ANOVA and Fisher's LSD tests to determine whether trees from the four regions differed in basal area, seed production, insect damage, foliar C : N, and tannin content. These ANOVAs had a single four-level predictor for region. We used an additional sequential ANOVA (i.e. type I) to investigate the variability in basal area among genotypes after regional differences were factored out. This ANOVA had a single four-level predictor for region and a 34-level predictor for source tree.

## RESULTS

Native genotypes were less vigorous than invasive genotypes. Basal area (Fig. 1A) and the likelihood of producing seed after 14 years (Fig. 1B) depended significantly on geographical origin of genotype. Native genotypes were smallest, genotypes from areas more recently colonized were largest and genotypes from the area of introduction were intermediate in size (Fig. 1A). The magnitudes of the differences in size and seed production were large (Figs 1A,B). In the sequential ANOVA, region accounted for 43.6% of the variability in basal area, and source tree accounted for an additional 10.7% of the variability (ANOVA  $F_{30,330} = 13.1$ ,  $P < 0.0001$ ; region  $F_{3,330} = 105.0$ ,  $P < 0.0001$ ; source tree  $F_{27,330} = 2.87$ ,  $P < 0.0001$ ).

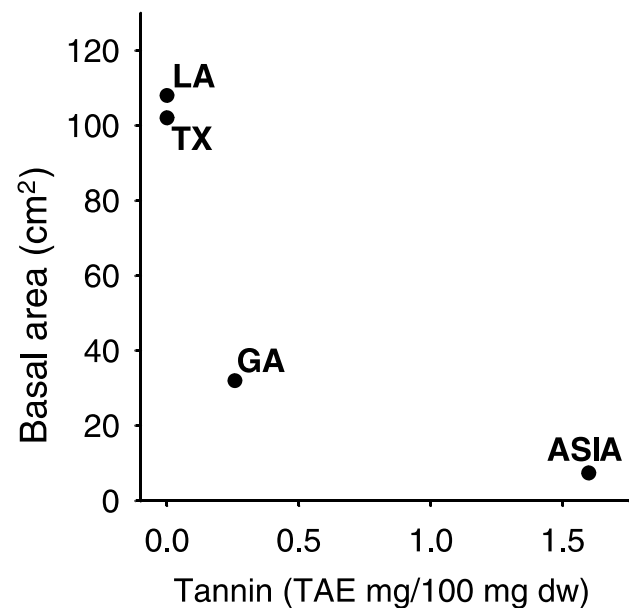
Despite their lower growth, native genotypes had the highest quality, best defended foliage. Native genotypes had the lowest foliar carbon to nitrogen ratios (C : N), genotypes from recently colonized areas had the highest ratios and genotypes from the area of introduction had intermediate C : N ratios (Fig. 1C). Although the range of C : N values in our study is probably too small to reflect ecologically significant differences in nitrogen limitation or nutritive value to herbivores (Elser *et al.* 2000), it does suggest that native genotypes are constructing tissues higher in proteins and/or nitrogen-based defensive compounds (Coley *et al.* 1985; Bazzaz *et al.* 1987). Concentrations of tannins (a carbon-based compound; Feeny 1970; Bazzaz *et al.* 1987) were highest in native genotypes, undetectable in

genotypes from recently colonized areas and intermediate for genotypes from the site of introduction (Fig. 1D). The tannin concentrations in Asia and Georgia genotypes were high enough to potentially deter herbivores (Feeny 1970, Hagerman 1987). However, all genotypes had extremely low amounts of leaf area removed by insect herbivores (average 0.24%) and the amounts were independent of genotype ( $F_{3,28} = 1.1$ ,  $P = 0.35$ ).

The higher tannin concentrations in native genotypes suggest that differences in growth do not simply reflect a physiological or phenological mismatch to the local climate (Williamson 1996; Lonsdale 1999). Maternal effects (i.e. non-genetic differences in seed quality) can also cause differences in performance, especially in the earliest stages of growth (Nelson *et al.* 1970; Willis *et al.* 2000). However, height at the end of the second year of the experiment was independent of genotype ( $F_{3,357} = 1.39$ ,  $P = 0.25$ ), so maternal effects are not likely to explain our results.

## DISCUSSION

The EICA hypothesis is consistent with the high growth and low defence of our invasive genotypes (Fig. 2). However, these adaptations may be transitory. Initially, when native herbivores do not recognize and exploit them,



**Figure 2** Genetic differences in growth and defence of *Sapinum*. Native Asian genotypes had high foliar concentrations of defence chemicals and low growth. Genotypes from the site of introduction (GA) had lower defence and higher growth. At the further extent of its range in areas where it has recently become a serious invader of a variety of ecosystems (LA, TX), the decreases in defence and increases in growth are more extreme.

plants may be selected to allocate more to growth and reproduction (Strong *et al.* 1984; Chew & Courtney 1991; Adler 1999). As herbivores begin to utilize this abundant, edible resource, plants may be selected to allocate increasingly to defence (Strong *et al.* 1984; Chew & Courtney 1991; Adler 1999). The intermediate position of genotypes from Georgia, where *Sapium* was introduced to North America (Bruce *et al.* 1997), suggests that there may have been such a loss and reacquisition of defences in that geographical area.

Our results support the idea that evolutionary change by introduced species may play an important, but often underappreciated, role in invasions (Blossey & Notzold 1995; Daehler & Strong 1997; Willis *et al.* 1999; Mack *et al.* 2000; Willis *et al.* 2000; Mooney & Cleland 2001; Thebaud & Simberloff 2001). Indeed, dynamic allocation patterns may account for the variable results of previous authors if they were focusing on different times in the cycle of invasion and enemy pressure. Our results also suggest that lags from introduction to emergence as a problem invasive species may reflect a genetic adjustment period by the introduced plant and not just simple demographic lags (Crawley 1987; Mack *et al.* 2000). This will potentially complicate attempts to predict future invaders because the initial success of an introduced species may be a poor indicator of its ultimate success and ecological significance.

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#### **BIOSKETCH**

Evan Siemann is a population and community ecologist who studies plants and animals.