Ecological Applications, 13(6), 2003, pp. 1503–1507

INCREASED COMPETITIVE ABILITY OF AN INVASIVE TREE MAY BE LIMITED BY AN INVASIVE BEETLE

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Abstract. Invasive plants are often more vigorous in novel habitats than in their native ranges. *Sapium sebiferum* (Chinese tallow tree) is a major invader of habitats in the southern United States. Long-term common garden experiments in Texas and Hawaii (USA) with *S. sebiferum* genotypes from its native range (Asia) and from areas in North America where it is invasive suggest that post-introduction evolutionary changes may contribute to its invasiveness in Texas. In Texas, where there was uniformly low herbivory, fast-growing, poorly defended invasive North American genotypes outperformed slower growing, better defended native Asian genotypes in common garden plots. In Hawaii, in contrast, an Asian herbivore, *Adoretus sinicus* (Chinese rose beetle) is abundant, and *S. sebiferum* is not invasive. In Hawaiian common garden plots, *A. sinicus* caused greater damage to North American genotypes, and Asian genotypes were competitively superior. Our results suggest that exotic plants freed from herbivory can evolve greater competitive ability, allowing them to become much more abundant than in their native ranges. This did not seem to occur, though, if herbivores from the native range were abundant.

Key words: Adoretus sinicus; *biological invasions; Chinese tallow tree; evolution of increased competitive ability; Hawaii, USA;* Sapium sebiferum; *Texas, USA.*

INTRODUCTION

Invasions by alien plant species are a contemporary and future environmental threat (Mack et al. 2000, Pimentel et al. 2000). Invasive plants are often larger in introduced ranges than native ranges (Elton 1958, Crawley 1987, Blossey and Nötzold 1995, Mooney and Cleland 2001). This may reflect innate competitive superiority of the invasive plant (Darwin 1859, Lodge 1993, Lonsdale 1999, Tilman 1999) or a phenotypic response to low losses to herbivores in the introduced range (Elton 1958, Lodge 1993, Yela and Lawton 1997, Mooney and Cleland 2001, Keane and Crawley 2002). Another hypothesis (‘‘evolution of increased competitive ability hypothesis’’ or ‘‘EICA hypothesis’’; Blossey and Nötzold 1995) proposes that invasive plants evolve increased competitive ability in their introduced ranges by shifting resources from defenses to growth in response to chronically low losses to herbivores (Crawley 1987, Daehler and Strong 1997, Willis et al. 1999, Siemann and Rogers 2001, 2003). Not only does this hypothesis provide an explanation for the increased size of invasive plants, it may also explain other characteristics of invasions such as the high abundance of invasive plants, and it is the only one of these hypotheses that includes a mechanism which could give rise to the lag between the introduction of such species and their spread across a novel habitat (Mack et al. 2000). The EICA hypothesis, but not the others, predicts that invasive and native plant genotypes will have different growth rates in a common garden and that the invasive genotypes will be less well defended. In a common garden where herbivores from the plant's native range are absent, invasive genotypes should outperform native genotypes. However, native genotypes should outperform invasive genotypes in common gardens where herbivores from the plant's native range are abundant.

Focal species

In many southern U.S. ecosystems, Chinese tallow tree (*Sapium sebiferum* L., 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 purposely introduced to Georgia in the late 18th century from Asia for agricultural purposes and later to Texas and Louisiana by the U.S. 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. An ideal test of the

Manuscript received 21 January 2003; revised 6 March 2003; accepted 25 March 2003. Corresponding Editor: M. Rees.

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EICA hypothesis would compare individuals from an invasive population and individuals from the native population(s) that were the known original source population. This information is not known for *Sapium*. The first record of *S. sebiferum* in Hawaii, where Asian herbivores are abundant (Asquith and Messing 1993), dates to the 1920s (Bishop Museum specimen collected in 1927, North Kohala, Hawaii), but fewer than 100 trees are documented in the islands prior to 1980. In ideal conditions, *Sapium* reaches reproductive maturity in as little as two years (Grace 1998).

In 1985 and 1986, *S. sebiferum* trees were planted in common gardens in Hawaii (HI) and Texas (TX), USA, respectively. Each common garden received *S. sebiferum* trees grown from seed collected in Asia or North America. If *S. sebiferum* has evolved increased competitive ability in North America, invasive (North American) genotypes will be faster growing and less well defended than native (Asian) genotypes. In the common garden where herbivores from the plant's native range are rare (TX), invasive genotypes will outperform native genotypes whereas native genotypes will outperform invasive genotypes in the common garden where herbivores from the plant's native range are abundant (HI). We report growth, insect damage, and leaf chemistry data from 2002.

METHODS

Common elements of field experiment designs

In 1985 and 1986, fields in Honolulu County, HI, and Galveston County, TX, respectively, were rototilled and planted with *S. sebiferum* seedlings at a density of one per 1.5 m^2. These were grown in local greenhouses using seeds collected from trees in Asia (32 [HI experiment] and 14 [TX experiment] source trees in Taiwan) and North America (30 [HI experiment] and 14 [TX experiment] source trees in Texas). Three source trees from Texas were represented in both gardens but all other genotypes were planted only in a single garden. These experiments were originally established by Simco, Weston, Connecticut, USA, to study *S. sebiferum* as a potential oilseed crop. In these densely planted common gardens, there was competition among plants so the results from these studies indicate only relative performance of the genotypes at a site. If the trees had been grown sufficiently far apart so that they would not have competed, we could have tested the additional prediction of the EICA hypothesis that absolute performance of *Sapium* would be higher in Texas where herbivory was low.

Additional details of Hawaii design

All trees of each genotype were planted in contiguous groupings. In total there were 672 trees (176 Asian, 496 North American) with a range from 1 to 30 trees of each genotype. After 24 mo, saplings were pruned to ~1 m height and allowed to regrow. Data collected in the first few years were never published and are lost (Simco, *personal communication*). No data were collected again until the 17th year.

Additional details of Texas design

The original experimental design was randomized with 16 trees from each source tree, but Galveston County removed some trees from one end of the experiment in the 8th year, leaving an average of 11 trees per source tree. Some results from the 14th year and more details of the experimental design have been reported previously (Siemann and Rogers 2001).

Data collection

In May 2002, diameter at breast height (dbh, 137 cm) was measured for all living stems of each tree. From this we calculated basal area for each tree. We visually classified the amount of leaf area removed by chewing insects into five categories (see Fig. 1B). In the Hawaii common garden, we clipped leaves from all non-border row trees that had foliage below the height of 2.5 m (North America $N = 35$, Asia $N = 28$). The leaves were dried, ground, and analyzed for tannin content using the radial diffusion protein precipitation method (Hagerman 1987) with a tannic acid standard. From this set of leaves, we randomly chose six trees of Asian genotypes and six trees of North American genotypes and analyzed the leaf material for total nonstructural carbohydrates using the anthrone reagent method (Conway et al. 1999). In 2000, we analyzed foliar tannins in the Texas common garden (Siemann and Rogers 2001).

Analyses

We used separate ANOVAs for each common garden to test whether Asian or North American genotype trees differed in basal area or amount of chewing insect damage. For the blocked Hawaii design, we used the average of all of the trees grown from the seeds of each source tree as data points ($N = 62$). This is a conservative way to analyze these data. For the Texas garden, 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. The Hawaii garden experimental design did not allow us to perform this additional analysis.

RESULTS AND DISCUSSION

In the Texas garden, Asian genotype trees were significantly smaller than North American genotype trees ($F_{1,312} = 230.0$, $P < 0.0001$, Fig. 1A). If this design was analyzed with the average size of each source tree as a single data point, these differences would still be significant ($F_{1,30} = 176.1$, $P < 0.0001$). In the Hawaii garden, the growth pattern was reversed; Asian genotype trees were significantly larger than North American genotype trees ($F_{1,60} = 10.5$, $P < 0.01$, Fig. 1A). The larger size of Asian genotypes in Hawaii compared

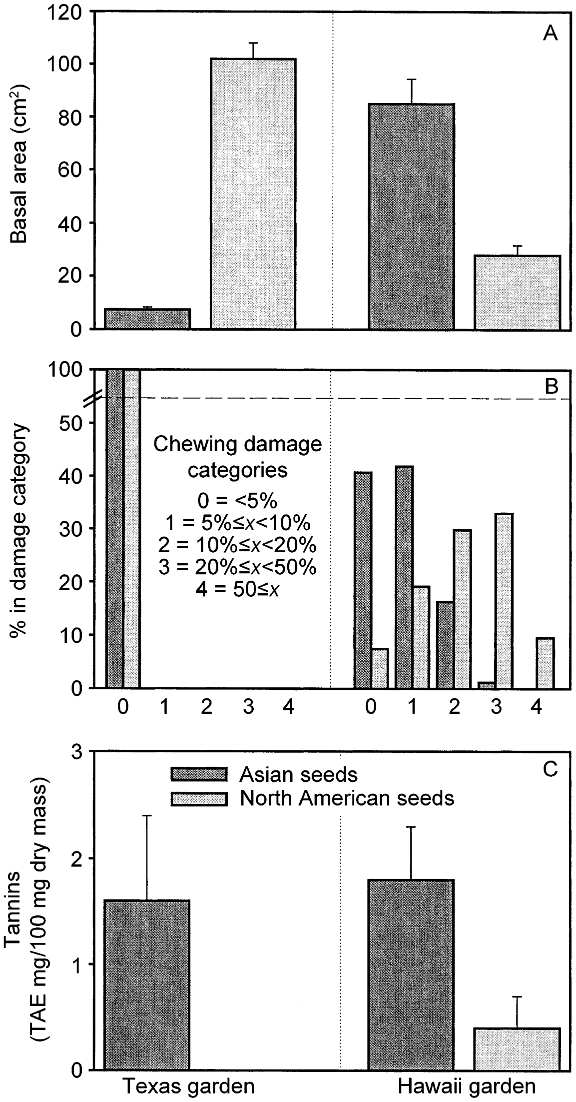

FIG. 1. Genotypes of *Sapium sebiferum* differed in (A) size and (B) amount of leaf area removed by chewing insects in competitive common gardens in Texas and Hawaii. (C) Asian genotypes had higher concentrations of tannins in each common garden. Error bars in (A) and (C) are means + 1 SE. These results show the relative performance of genotypes within a garden but do not indicate the relative growth potential of a genotype across gardens. TAE denotes tannic acid equivalent.

to Texas does not indicate better absolute performance of Asian genotypes at this site, but rather their performance relative to North American genotypes in the densely planted competitive gardens.

Alternative explanations for the differences we observed seem less likely than post-introduction evolution. Nongenetic differences in seed quality (i.e., maternal effects) can affect performance, especially in early stages of growth (Steinger et al. 2000, Willis et al. 2000). However, genotypes in the Texas garden did not differ in height in the second year ($F_{1,312} = 1.39$, $P = 0.24$) so maternal effects are not likely to be causing the differences in genotypes in later years. It is possible that a rare genotype founder effect was responsible for the genetic differences we observed, and there has been little or no genetic change following introduction (i.e., the original source material was from the same range as the new Asian material but the original source trees were unusual within that population). However, continent accounted for 42.4% of the variability in basal area in the Texas garden whereas source tree accounted for only 12.4% of the variability (ANOVA $F_{27,286} = 12.9$, $P < 0.0001$; region $F_{1,286} = 268.5$, $P < 0.0001$; source tree $F_{26,286} = 3.0$, $P < 0.0001$). The strong effect of continent compared to source tree indicates that performance differences are more likely attributable to post-introduction genetic change than to a rare genotype founding the North American *Sapium* populations. However, the absence of a rare genotype effect can never be demonstrated conclusively without more information about the original plants than is known for *Sapium*. It is also possible that *Sapium* varies in growth and defense within its broad native range, and *Sapium* in the original source populations (unknown geographic location) have always been fast growing and poorly defended. We did not sample *Sapium* across a broad geographic range (i.e., continental) and cannot dismiss this possibility. In addition, a phenotypic response to low herbivory would not explain why the genotypes differed within the Texas garden (Tilman 1999, Keane and Crawley 2002). Last, the differences in growth and defense that we observed are consistent with natural selection for plants with high growth rates and low defense allocation in an environment with low herbivory, but these differences could also reflect artificial selection for rapid growth in the introduced range.

In the Texas garden, Asian and North American genotype trees were all in the lowest category of insect chewing damage (Fig. 1B). However, in the Hawaii garden, North American genotype trees were significantly more damaged than Asian genotype trees ($F_{1,50} = 64.7$, $P < 0.0001$, Fig. 1B). The herbivore that appeared to be causing most of the damage was *Adoretus sinicus* Burmeister (Coleoptera: Scarabaeidae), a generalist chewing folivore that feeds on >250 species of plants in Hawaii (Habeck 1963). It is not known when this insect was introduced from Asia, but it was a pest of Hawaiian sugarcane fields by the beginning of the 20th century (Habeck 1963). Its range in Asia includes southeast Asia, Taiwan, and Japan (Clausen 1978). A congener *A. tenuimaculatus* Waterhouse occurs in mainland China and is known to cause heavy damage to *Sapium* (Zhang and Lin 1994).

The amount of nonstructural foliar carbohydrates is an important factor in the food selection of *A. sinicus* (Arita et al. 1988), but Asian and North American genotypes did not differ in this respect (t test, $P = 0.35$). Differences in defense chemical concentrations may also influence food selection by herbivores (Pavia et al. 2002). The amounts of foliar tannins were significantly greater (*t* test, $P < 0.05$) in Asian genotypes than in North American genotypes (Fig. 1C). The differences in tannin concentrations we observed here are large enough to be ecologically significant (Feeny 1970) and are consistent with *A. sinicus* preference for North American genotypes in the Hawaiian common garden.

The patterns of growth, damage, and defense (Fig. 1) suggest that preferential feeding by *A. sinicus* may have caused the differences in relative performances of genotypes in Hawaii and Texas. Although these results match the predictions of the EICA hypothesis, until further manipulative experiments have been carried out, we cannot know definitively whether the differences in herbivore damage were indeed the cause of performance disparities or if herbivores may have fed on plants that lacked vigor for other reasons. For instance, it is possible that differences in soil, climate, mutualists, and/or pathogens between Hawaii and Texas were the cause of the reversal in competitive abilities in the common gardens. Reductions in defense likely 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). This may explain why some plant species are much more abundant in a novel than a native habitat and why some plants are invasive in one habitat but not in another.

Our results are strong preliminary evidence that herbivores may influence plant invasions by an evolutionary shift of resources away from defenses and toward growth (Blossey and Nötzold 1995, Mack et al. 2000, Mooney and Cleland 2001). Geraniin, a hydrolyzable tannin, is a major defensive compound found in *Sapium* leaves (Neera et al. 1992). Because the two main pathways for hydrolyzable tannin synthesis are the phenylalanine and tryptophan pathways (Kanehisa 2000), protein synthesis likely competes directly with tannin synthesis, thereby potentially generating a growth vs. defense trade-off in *Sapium* (Zucker 1983, Arnold and Schultz 2002).

The reversal of genotype success in the two common gardens suggests that the same evolutionary changes that are effective with naïve herbivores in the introduced range may not be an advantage in the presence of herbivores from the native range (Fig. 1). This scenario may be relevant to the introduction of a biological control agent. It is often assumed that the success of biological control agents reflects a restoration of feeding relationships from the native range (Knight 2001). Rather, successful biological control may indicate an unusually vulnerable host plant that is poorly defended against its herbivores. Greater consideration of biological invasions in both evolutionary and ecological terms (Thompson 1998, Thomas et al. 2001) may lead to greater accuracy in predicting future invaders (Kolar and Lodge 2001) and may aid in developing methods of control for problem species.

ACKNOWLEDGMENTS

We thank: R. Boom, B. Butterfield, E. Glumac, R. Lankau and D. Mee for assistance; D. Tilman for comments; the University of Houston Coastal Center and the University of Hawaii Waimanalo Research Station for access; and the U.S. National Science Foundation (DEB-9981654) for support.

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