

Rapid adaptation of insect herbivores to an invasive plant

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Introduced plant success often is attributed to release from natural enemies in their new ranges. However, herbivores may accumulate over time and reduce invasiveness but evidence for this process to date is weak. We report here that enemy release is indeed limited to the early stages of introduction of the Chinese tallow tree (*Sapium sebiferum*). In bioassays and gardens along a geographical gradient of time since tallow tree introduction, herbivory was highest and tree performance was poorest where tallow tree has been present longer (i.e. introduced earlier). Additionally, Asian ecotypes (grown from seeds collected in Asia) had lower survival than North American ecotypes (seeds collected in North America), which is consistent with genetic responses to low herbivory in the introduced range (EICA Hypothesis). Release from insect herbivores appears to contribute to early success of the tallow tree, but accumulation of insect herbivores has apparently reduced this benefit over time.

Keywords: biological invasions; Chinese tallow tree; herbivore accumulation; *Sapium sebiferum*

1. INTRODUCTION

The spectacular success of introduced plants is widely believed to reflect low pest loads in their introduced ranges (Elton 1958; Yela & Lawton 1997; Mack *et al.* 2000; Maron & Vila 2001; Keane & Crawley 2002; Mitchell & Power 2003). A release from enemy attack may benefit invasive plants relative to native plants both through phenotypic responses to benign conditions (Mack *et al.* 2000; Maron & Vila 2001; Keane & Crawley 2002) and by evolutionary shifts in allocation from defence to growth and reproduction (Blossey & Nötzold 1995; Bosdorf *et al.* 2005). Yet, studies of crop plants and introduced trees have shown that they have a diversity of insect herbivores comparable to native species within 350 years of their introduction (Strong 1974a,b; Strong *et al.* 1977; Leather 1986; Andow & Imura 1994). Together these findings suggest a complex interaction of native herbivores and introduced plants in which low levels of herbivory at first may promote invasion success but then accumulation of herbivores over a period of centuries eventually equalizes invasive and native plant performance (defined here as naturalization). We present results from a study of the Chinese tallow tree (*Sapium sebiferum*) that is a strong evidence that such a sequence of initially low herbivory then slow accumulation of herbivores plays an important role in initial success and eventual naturalization (Rosenzweig 2001).

The tallow tree presents an extraordinary opportunity to study the process of herbivore accumulation because its invasive success is influenced by both phenotypic and genetic responses to low herbivore loads in its introduced range (Siemann & Rogers 2001, 2003a,b) and it has a well documented invasion history with a variation in time

present from 100 to 233 years among sites in North America (Bruce *et al.* 1997). Long-term common gardens have shown higher growth rates and lower defence levels in tallow tree ecotypes from its introduced range compared to its native range with the contrast most striking for trees from areas where it has been more recently introduced (Siemann & Rogers 2001). This suggests there may be important variation in herbivore pest loads along a biogeographical gradient that represents time since introduction and that variation in herbivore loads may influence plant traits and invasive potential.

In 2003, tallow tree seedlings grown from seeds collected in its native range (Asia), site of North American introduction (Georgia (1772)) and areas of later introduction (Florida (approx. 1865), Louisiana (approx. 1900) and Texas (approx. 1900)) were planted in common gardens in open, prairie-like vegetation in Georgia, Florida, Louisiana and Texas. These sites have similar climates. We have not identified the native origin of introduced material into the US, but genetic analyses using microsatellites (DeWalt *et al.* 2006) suggest that Georgia ecotypes stem from a different source population to Texas, Louisiana and Florida ecotypes (S. J. DeWalt 2006, unpublished data). Our common gardens also included seedlings of the native trees sweetgum (*Liquidambar styraciflua*) and hackberry (*Celtis laevigata*) that occur in all four sites to control for differences in herbivore conditions unrelated to time of tallow tree presence. We collected data on survival, height growth rates and plant size for two growing seasons to compare the performance of native tree seedlings versus tallow tree seedlings in these locations that differ in the amount of time tallow trees have been present (Bruce *et al.* 1997). If accumulation of pests over time reduces growth and survival, tallow tree performance should be weakest compared to natives in the Georgia garden.

In 2003 and 2004, we conducted short-term insect herbivory bioassays with tallow tree and native tree

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seedlings to measure the potential herbivore pressure on seedlings in the four North American locations where tallow tree has been present for different periods of time (Georgia, Florida, Louisiana, Texas). We used seedlings of uniform condition (i.e. similar height and no previous insect damage) grown from seeds collected across the southeastern US and China. If pests have accumulated on tallow tree where it has been present for a longer time, herbivore damage should be highest relative to natives in sites where it has been present the longest (Georgia).

2. MATERIAL AND METHODS

(a) *Seeds*

From November 2002 to January 2003 and from November 2003 to January 2004, we hand collected seeds from Chinese tallow tree (*S. sebiferum* (L.) Roxb., Euphorbiaceae, synonyms include *Triadica sebifera*) trees in the southeast US (five states—Texas, Louisiana, Florida, Georgia and South Carolina) and southeast China (five provinces—Jiangxi, Anhui, Zhejiang, Hunan and Taiwan). Since all of the trees in South Carolina were within 5 km of the Georgia border and they were genetically similar to Georgia trees (DeWalt *et al.* unpublished data), we combined Georgia and South Carolina seeds into one category for all analyses. In November 2002 and 2003, we collected seeds from hackberry (*C. laevigata*) and sweetgum (*L. styraciflua*) trees in Texas.

(b) *Seedlings*

Seeds were stored at room temperature until March 2003 (2002 collections) or March 2004 (2003 collections). They were then washed in water and laboratory glassware detergent to remove the outer waxy seed coat. A sub-set of the seeds from each parent tree was weighed as individual seeds that were tracked throughout the experiments in order to evaluate the potential contribution of seed provisioning to seedling performance (i.e. non-genetic heritable differences). Since the wax coat on the outside of the seed is unrelated to provisioning for the plant embryo, it had to be removed prior to weighing seeds. Seeds were planted into 115 ml containers (Stuewe & Sons, Corvallis, OR) filled with commercial topsoil mix in an unheated greenhouse in Houston, Texas.

(c) *Common gardens*

In June 2003, common gardens were planted in each of four locations (Georgia: University of Georgia Marine Institute, McIntosh County; Florida: Florida State University Mission Road Station, Leon County; Louisiana: University of Louisiana Centre for Ecology and Environmental Technology, Lafayette Parish; Texas: University of Houston Coastal Centre, Galveston County). Each garden had 160 seedlings (20 hackberry, 20 sweetgum, 120 tallow tree (20 Asia, 40 Georgia, 20 Florida, 20 Louisiana, 20 Texas)) planted in a randomized design in a 32×5 m grid. We measured the height of each seedling at planting. Each area was dominated by graminoids and broadleaf herbs. The background vegetation was not managed during the course of the experiment but each had been mowed shortly before planting.

We checked seedling survival and measured seedling height five times during the 2003 and 2004 growing seasons. We had initially intended to have the experiment continue

until the end of the 2005 growing season, but after two growing seasons, the tallest tallow tree 'seedling' was 1.5 m tall (and nine more were taller than one metre). Since tallow trees can begin to flower once they reach a height of 2 m and we did not want to contribute genetically novel pollen or seeds to North American populations, we were only able to run the common gardens for two growing seasons. In September 2004, we harvested seedlings and then dried and weighed them. We used sequential ANOVAs to test whether seedling survival time (days since planting), seedling height growth rate ($\ln(\text{final height}/\text{initial height})/\text{days since planting} \times 1000$), or seedling mass (log transformed to meet assumptions of normality) depended on: location (Georgia garden, Florida garden, Louisiana garden or Texas garden), Status (tallow tree versus native), status×location, ecotype (tallow tree seeds from native range or introduced range), ecotype×location, state (tallow tree seeds from Georgia, Florida, Louisiana or Texas), state×location, tree (identity of tallow tree parent tree), native (sweetgum or hackberry) and native×location. A sequential ANOVA had to be used because the hierarchical structure of the predictors precluded using Type III sums of squares. We used adjusted means contrasts to test for differences among levels of predictors that had a significant effect on the response variable and that had more than two levels. We used regression to test whether seed mass predicted seedling heights 28 days after germination, at time of planting or at the end of the first growing season. Seedlings grown from heavier seeds were taller 28 days after germination ($p < 0.0001$), but height did not depend on seed weight by the time seedlings were planted in the gardens ($p = 0.07$) or at the end of the first growing season ($p = 0.18$).

(d) *Short-term herbivory bioassays*

Twice during each growing season (June 2003, July 2003, June 2004, July 2004), seedlings were planted into short-term arrays in open, prairie-like vegetation at each site. The initiation date varied by four to seven days among sites for each set. Each array had 56 seedlings (896 total). Since the number of healthy, undamaged seedlings available was not even across genotypes, the design was unbalanced with regard to genotype. Each assay had on average: 6 hackberry, 8 sweetgum and 42 tallow tree (3 Asia, 7 Florida, 16 Georgia, 8 Florida, 8 Louisiana, 8 Texas) seedlings. Prior to planting we measured the height and counted the leaves of every seedling. Seedlings were planted in their containers in a randomized design in a 1 m spaced grid. Fourteen days later, we collected the seedlings, measured their heights and, counted their leaves. All leaves were then removed, scanned on a flatbed scanner, and leaf area removed by chewing insects was determined using SCION IMAGE.

We used a sequential ANOVA to determine whether the percentage of leaf area removed depended on: set (June 2003, July 2003, June 2004, July 2004), location, status, status×location, ecotype, ecotype×location, state, state×location, native and native×location. Since an abundance of zeros causes problems in ANOVAs by creating non-normal distributions that cannot be transformed to achieve normality, we only included seedlings that had some insect chewing damage. In addition, seedlings that were browsed by rodents were excluded from the analyses of insect damage since only a short stem base remained. We used adjusted means contrasts to test for differences among levels of significant predictors with more than two levels. We used logistic regression to test

whether the odds of a seedling being browsed by rodents or the odds of a seedling experiencing leaf area removal depended on the same set of predictors as in the ANOVAs. All analyses were done using SAS v. 9.1.

3. RESULTS AND DISCUSSION

As expected for a successful invader, average survival time was longer for tallow tree seedlings (284 ± 9 days) than for native tree seedlings (230 ± 15 days) and the average tallow tree seedling grew faster (figure 1a) and was larger at the end of the experiment compared to native tree seedlings (table 1 'status' term, 145 ± 28 g for native seedlings and 1245 ± 119 g for tallow tree seedlings) in the common gardens. However, this did not represent a global superiority of tallow tree versus native trees such that it outperformed them in all locations. Rather, tallow trees had a substantial advantage compared to natives in terms of growth rate only in the two locations where it has been more recently introduced (Texas and Louisiana, table 1 'status $\times$ location' term). In fact, tallow tree had a lower growth rate than natives in the two locations where it has been present for a longer period of time (figure 1a). There are many possible explanations for this pattern, such as differences in soil types (Barrilleaux & Grace 2000), moisture (Burns & Miller 2004; Butterfield *et al.* 2004) or environmental conditions (Rogers & Siemann 2002; Siemann & Rogers 2003c) among sites, but results of herbivory bioassays indicated that pest accumulation likely plays a role in this reversal of tallow tree and native performances in at least the Georgia site. Since seedling survival and growth can determine plant population dynamics (Crawley 1996), these results for seedlings may indicate tallow tree invasion pressure in these locations as well.

In the two-week herbivore bioassays, tallow tree seedlings suffered less chewing damage on average than did native tree seedlings but damage was higher for tallow trees than for natives in Georgia (figure 1b, table 2 'status' and 'status $\times$ location' terms). If other types of herbivory, such as leaf mining, phloem feeding, or root feeding, or diseases which are all common in its native range (Zhang & Lin 1994) show a pattern that is similar to that for leaf chewing insects, the impact on tallow tree vigour and its ability to invade a broad range of habitats could be substantial (Crawley 1996). Indeed, surveys of damage in replicate monocultures of tallow tree and three native tree species in Texas (sweetgum, silver maple (*Acer saccharinum*), sycamore (*Platanus occidentalis*)) showed that the amounts of leaf mining damage were far lower on tallow than on any native species (M. K. Hartley 2006, unpublished work), which is consistent with our results for Texas gardens and chewing damage. The levels of mining damage in Georgia are unknown. More generally, the rates of accumulation of generalist herbivores on crop plants in Japan seem to be faster than for specialist herbivores such that the proportion of specialists in the insect herbivore fauna on those plants increases over a period of centuries (Andow & Imura 1994). The odds of a seedling being damaged depended on set ($p < 0.0001$) and native species ($p < 0.001$, hackberry more likely to be damaged than sweetgum) but was independent of all other predictors (location, $p = 0.22$; status, $p = 0.15$; status $\times$ location, $p = 0.75$; ecotype, $p = 0.32$;

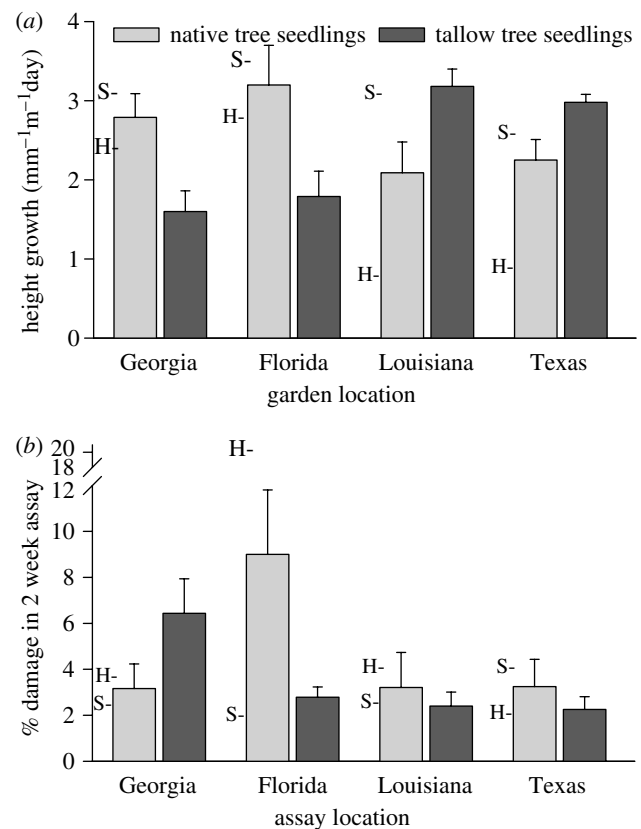


Figure 1. (a) The dependence of height growth rate of native tree seedlings and tallow tree seedlings in the four common gardens where tallow tree has been present for different periods of time (Georgia approx. 230 years, Florida approx. 140 years, Louisiana and Texas approx. 100 years). The average height growth rates for sweetgum and hackberry seedlings within each location are indicated by 'S' and 'H', respectively. The distances between species means and the average for natives may be uneven due to unbalanced numbers of surviving seedlings. (b) The amount of insect chewing damage experienced by native tree seedlings and tallow tree seedlings in four bioassay locations. Native species means are indicated by 'S' and 'H'.

ecotype $\times$ location, $p = 0.96$; state, $p = 0.37$; state $\times$ location, $p = 0.74$; native $\times$ location, $p = 0.10$). Overall, these results suggest that Georgia may represent a biotic environment that is intermediate between the areas where tallow tree has recently been introduced and its native range. This corresponds well with previous results showing the herbivore defence traits of Georgia ecotypes (foliar tannins) are intermediate between those of Asia versus Texas and Louisiana (Siemann & Rogers 2001).

The majority of the literature on herbivore accumulation has focused on herbivore diversity with comparatively little attention being paid to herbivore loads. Our data on herbivore loads agree with the literature on the dynamics of herbivore diversity. In contrast, Carpenter & Cappuccino (2005) found that time since introduction and amount of leaf damage were unrelated in a cross species comparison. However, the greater relative herbivore damage we observed at sites where tallow tree has been present longer may be consistent with the overall lack of a relationship between time since introduction and herbivore loads within a flora that they found. Indeed, every plant species could have an increasing herbivore load over time without a community level pattern existing if

Table 1. The dependence of survival time, height growth and mass after two growing seasons on common garden location (Texas (TX), Louisiana (LA), Florida (FL), Georgia (GA)), seedling status (tallow tree versus native), ecotype (tallow tree seeds from trees in Asia versus North America), state (tallow tree seeds from trees in Texas, Louisiana, Florida or Georgia), tree (identity of tallow tree parent tree) and native species (hackberry versus sweetgum) in sequential ANOVAs with interactions of location and status, ecotype, state and native. (Significant results are in bold. Differences among means are shown where the same letter denotes means that were indistinguishable at $p < 0.05$.)

factor	survival time			height growth rate			log (final mass)					
	d.f.	SS	F	p	d.f.	SS	F	p	d.f.	SS	F	p
location	3	75.8	74.3	<0.0001	3	40.6	1.7	<0.001	3	7.5	8.0	<0.0001
contrasts												
status	1	6.0	17.6	<0.0001	1	7.5	5.9	<0.05	1	36.0	114.5	<0.0001
status×location	3	0.9	0.8	0.45	3	29.5	7.8	<0.0001	3	7.6	8.2	<0.0001
ecotype	1	3.3	9.7	<0.01	1	4.9	3.6	0.06	1	0.1	0.5	0.49
ecotype×location	3	3.2	3.1	<0.05	3	0.6	0.2	0.93	3	0.1	0.1	0.95
state	3	0.6	0.6	0.62	3	11	2.9	<0.05	3	1.8	1.9	0.13
contrasts												
state×location	9	2.9	0.9	0.48	9	5.7	0.5	0.87	9	1.2	0.4	0.91
tree	182	2.7	0.1	0.99	62	96.4	1.2	0.15	62	25.0	1.2	0.10
native	1	3.1	9.1	<0.01	1	32.4	25.6	<0.0001	1	9.1	29.2	<0.001
native×location	3	4.0	3.9	<0.01	3	3.8	1.0	0.39	3	0.7	0.7	0.53
model	209	156.1	2.2	<0.001	89	232.5	2.1	<0.0001	89	88.8	3.2	<0.0001
error	430	146.2			170	215.3			170	52.9		

Table 2. The dependence of insect chewing damage in two week bioassays on set (June 2003, July 2003, June 2004, July 2004), assay location (Texas, Louisiana, Florida, or Georgia), seedling status (tallow tree versus native), ecotype (seeds from trees in Asia versus North America), state (seeds from trees in Texas, Louisiana, Florida or Georgia) and native species (hackberry versus sweetgum) in a sequential ANOVA with interactions of location and status, ecotype, state and native.

factor	d.f.	SS	F-value	p-value
set	3	9.6	3.7	<0.05
location	3	2.3	0.9	0.44
status	1	16.2	18.9	<0.0001
status×location	3	32.6	10.9	<0.0001
ecotype	1	2.3	2.6	0.11
ecotype×location	3	3.5	1.3	0.27
state	3	0.9	0.3	0.80
state×location	9	4.8	0.6	0.79
native	1	28.8	33.6	<0.0001
native×location	3	28.6	11.1	<0.0001
model	26	129.6	5.1	<0.001
error	192	164.6		

plant traits change through time (Blossey & Nötzold 1995) or introductions are not random such that different families, functional groups or paths of introduction characterize different time periods. The rapid loss and reacquisition of defence chemical production shown by *Pastinaca sativa* during a period of low herbivory followed by introduction of a coevolved herbivore, *Depressaria pastinacella*, from its native range is a good example of the potential complexity of the issue (Zangerl & Berenbaum 2005).

The odds of a seedling being browsed depended on only set ($\chi^2_3=75.6$, $p<0.0001$, order of odds ratios: 2003 second set > 2004 first set > 2004 second set > 2003 first set) and garden location ($\chi^2_3=30.2$, $p<0.0001$, order of likelihood of browsing Louisiana~Florida~Georgia>Texas) but not on status ($p=0.99$), status×location ($p=0.07$), ecotype ($p=0.98$), ecotype×location ($p=0.59$), state ($p=0.99$), state×location ($p=0.37$), native ($p=0.96$), or native×location ($p=0.20$). Although the interaction of status×location was not significant at $\alpha=0.05$, native tree seedlings were more likely to be browsed than tallow tree seedlings in Florida, Louisiana and Texas and were less likely than tallow tree seedlings to be browsed in Georgia. The probability of being browsed for native seedlings divided by the probability of a tallow tree seedling being browsed at that location (i.e. odds ratios) was equal to 0.44 in Georgia, 1.47 in Florida, 2.38 in Louisiana and 3.0 in Texas. These results are consistent with an accumulation of rodent browsing pressure in sites where tallow tree has been present longer compared to sites where it has been more recently introduced though the short time course of this study makes any conclusions regarding rodents very weak.

The two native tree species differed in their survival time, height growth rates and final mass (table 1, 'native' terms) with sweetgum having longer survival times, faster growth rates and larger final mass than hackberry. The general pattern of longer survival times for tallow tree than native species (table 1, 'status' term) held in the individual native species comparison since tallow tree had longer

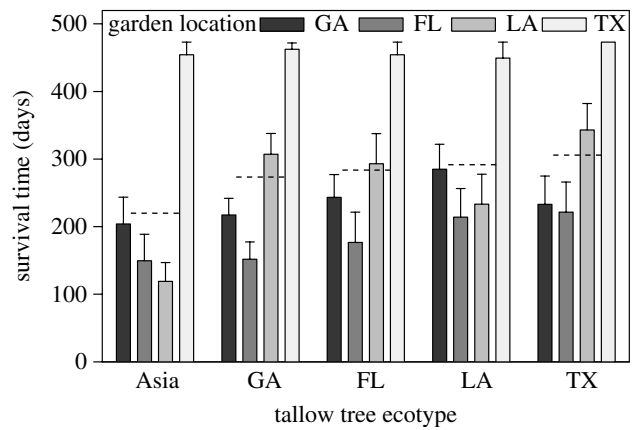


Figure 2. The average survival time of tallow tree seedlings of different ecotypes in the four common gardens (GA=Georgia, FL=Florida, LA=Louisiana, TX=Texas). The dashed lines indicate the average survival time for an ecotype across all four gardens. All Texas seedlings survived in the Texas garden.

average survival times than either native species. In addition, both native species had faster growth rates in Georgia and Florida than tallow tree seedlings did and tallow tree seedlings had faster height growth rates in Louisiana and Texas than either native species did (figure 1a, 'S' and 'H') which supports the pattern from the comparison of tallow tree to native species in general. Similarly, the same patterns for tallow tree and natives in general for final mass were also found for tallow tree and each native species. The patterns for individual native species and tallow tree for damage were not as clear as those for the comparison of tallow tree to native species in general because sweetgum seedlings received less damage than tallow tree seedlings in Florida and hackberry seedlings received slightly less damage than tallow tree seedlings in Texas (figure 1b, 'S' and 'H'). The strong pattern of higher damage on tallow tree seedlings than native seedlings in Georgia held for tallow tree and each native species. So, although there is variation between the two native plants, the pattern of tallow trees in terms of growth, survival and herbivore damage does not seem to depend critically on this variation.

For tallow tree seedlings, survival time was shorter for seedlings from Asia than for seedlings from North America (table 1, figure 2). This is consistent with results from long-term gardens in Texas that showed native ecotypes are better defended and slower growing than introduced ecotypes but that native ecotypes are less vigorous with the low levels of non-selective herbivory that are present in North America (Siemann & Rogers 2001). In fact, since the amounts of herbivory were similar across ecotypes in every location in this study (table 2, 'ecotype' term), the lower survival of native ecotypes would be expected given a dissociation of herbivore attack and defence production (Blossey & Nötzold 1995) and the lower herbivore tolerance of Asian ecotypes that is a consequence of these high costs of defence (Rogers & Siemann 2005). In addition, the greatest contrast between native and introduced ecotype survival was in Georgia where there were the highest amounts of damage (figure 1b). It is interesting to note, however, that in Hawaii where tallow tree has been present for 100 years and is not invasive, it suffers high levels of herbivory from

Asian insect herbivores that do discriminate between native and introduced ecotypes and preferentially cause especially heavy damage on introduced ecotypes (Siemann & Rogers 2003a). However, a fully adapted herbivore fauna may require substantially longer to develop than the two centuries tallow tree has been present in Georgia.

Although we are confident that there are genetically determined differences in performance between Asian and North American ecotypes (Siemann & Rogers 2001, 2003a,d; Rogers *et al.* 2003; Rogers & Siemann 2005), it is difficult to determine the cause of such differences. One possibility is directional selection on plant traits in low herbivore pressure conditions (Blossey & Nötzold 1995; Zangerl & Berenbaum 2005). Without knowing the closest contemporary Asian relatives to the North American populations in this study, it is not possible to determine whether there were preexisting differences among genotypes within Asia that have been preserved in introductions to North America. Nonetheless, we have since sampled genotypes throughout China and have not found consistent differences among populations in their growth rates either in common garden experiments in China or Texas (E. S. Siemann 2006, unpublished data).

Height growth depended on origin within the US (table 1, 'state' term). The growth rates of seedlings grown from seeds collected in Georgia were higher than some collected in other states (significant only for Georgia versus Florida), which suggests that there may be genetically determined variation in growth rates within the introduced range. Because Georgia and Gulf Coast populations appear to have distinct source populations in China (S. J. DeWalt 2006, unpublished data), this might reflect either preexisting differences among source populations or evolutionary change in the introduced range. However, in a long-term (14 year) common garden study in Texas, tallow trees from Texas grew faster than those from Georgia (Siemann & Rogers 2001) which is opposite to the pattern found here. The pattern of variation in growth rates among North American populations is unclear.

The results of our experiments along a chronosequence of introduction time indicate that tallow tree in Texas and Louisiana are still relatively herbivore-free compared to native trees with similar ecological requirements. In contrast, tallow trees in Georgia apparently have begun to accumulate herbivore loads comparable with native trees. These results would be strengthened by additional sites with long time periods since introduction. The period after introduction when plants experience low pest loads would be the period when there is the potential for selection against plant allocation to defences (Blossey & Nötzold 1995; Bossdorf *et al.* 2005). More generally, shortly following introduction, introduced plants may have unusual biotic interactions with a variety of components of the community that include not only pests but also interactions with other plants (Callaway & Ridenour 2004) and soil organisms (Klironomos 2002). Understanding the mechanisms that contribute to the success of invasive plants and the process by which they become incorporated into the local flora is critical given the current unprecedented rate of introductions and the consequences of these invasions for natural ecosystems.

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