Functional Ecology 2007
21, 721–730

Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*

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Summary

1. Functional traits contribute to the success of invasive plants. These traits can reflect inherent properties or they can be new adaptations from evolutionary responses to escape from natural enemies of the introduced range. We tested the hypothesis that genetic shifts in morphological and physiological traits have occurred between native and invasive populations of *Sapium sebiferum*.

2. *Sapium sebiferum* seedlings were grown in a greenhouse using seed collected from four populations of its introduced range (US) and four from native Chinese populations that are thought to be genetic candidates of the introduced populations. We examined plant biomass production, relative growth rate (RGR), relative stem height growth rate (RHR), root : shoot ratio (RSR), total number of leaves (TLN) and leaf area (TLA), specific leaf area (SLA), leaf area ratio (LAR), net CO_2 assimilation (A) and shoot specific respiration rate (R_D).

3. US populations of *S. sebiferum* differed from Chinese populations for most plant variables. Final shoot and total biomass, as well as, RGRs of invasive (US) populations were significantly greater than those of native (Chinese) populations, although RHR and TLN per seedling did not differ between them. Root : shoot ratios (RSR) were significantly lower, while leaf traits including TLA, LAR and SLA were generally greater for invasive populations compared to native populations. Net CO_2 A was significantly higher for invasive populations than for native populations, but no significant difference in R_D was found between two population types.

4. Of 13 measured plant variables, RSRs, TLA and CO_2 A were identified as traits that contributed the most to differences observed between native Chinese and invasive US populations. The suite of morphological and physiological traits functioning together may result in different growth strategies for native versus invasive populations. By virtue of these traits, invasive populations of *S. sebiferum* may use soil resources and light more efficiently than native populations, which may have given rise to their competitive superiority in the introduced range.

Key-words: biomass allocation, common garden, evolution of increased competitive ability, invasive species, plant traits

Functional Ecology (2007) **21**, 721–730
doi: 10.1111/j.1365-2435.2007.01298.x

Introduction

Invasive plants often grow more vigorously and attain higher abundances in their introduced range compared to conspecifics in their native range (Elton 1958; Crawley 1987; Thebaud & Simberloff 2001; Leger & Rice 2003; Jakobs, Weber & Edwards 2004; Bossdorf *et al.* 2005). To identify factors contributing to their invasive success, a number of studies have investigated morphological and physiological traits of invasive plants by comparing them with the native species they displace or non-invasive congeners (e.g. Roy 1990; Rejmánek & Richardson 1996; Williamson & Fitter 1996; Reichard & Hamilton 1997). In these studies and others, greater relative growth rates (RGR) of introduced species are generally associated

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with lower root : shoot ratios (RSR), higher specific leaf areas (SLA; leaf area per unit leaf mass), leaf area ratios (LAR; total leaf area per unit plant mass) and higher net CO_2 assimilation (A) as well as lower respiration costs (R_D) (Pattison, Goldstein & Ares 1998; Baruch & Goldstein 1999; Durand & Goldstein 2001; Smith & Knapp 2001; Grotkopp, Rejmánek & Rost 2002; McDowell 2002; Ehrenfeld 2003; Wilsey & Polley 2006).

These functional traits, common to invasive plants, may reflect their inherent properties due to previous evolution in the native range before its introduction or new adaptation as a result of an evolutionary response to escape from natural enemies in the introduced range (Blossey & Nötzold 1995; Callaway & Aschehoug 2000; Leger & Rice 2003; Erfmeier & Bruelheide 2005; Güsewell, Jakobs & Weber 2006). Some invasive plants may be innately better competitors because they evolved in a more competitive environment (Crawley 1987; Tilman 1999; Callaway & Aschehoug 2000; Davis, Grime & Thompson 2000). Once established in the introduced range, they may gain a systematic advantage over competitively inferior native plants. On the other hand, since allocation to defence may be as costly as herbivore damage (Bazzaz *et al.* 1987; Baldwin, Sims & Kean 1990), plants that escape their enemies in an introduced range could gain a selective benefit from decreasing their defensive investment. As a consequence, they may evolve to be fast-growing and low herbivore-defence plants (EICA hypothesis, Blossey & Nötzold 1995; Thompson 1998; Mooney & Cleland 2001). The distinction between environmentally induced phenotypic differences and a genetic change could be revealed by common garden experiments in which both native and invasive individuals are grown together in the same environment (Siemann & Rogers 2001; Leger & Rice 2003; Wolfe, Elzinga & Biere 2004; Erfmeier & Bruelheide 2005; Güsewell *et al.* 2006).

While the majority of past studies have compared invasive plants with natives or non-invasive congeners, only a few common garden studies have concentrated on variation in morphological and physiological traits between native and invasive populations of exotic plants (Bastlová & Kvêt 2002; DeWalt, Denslow & Hamrick 2004; Erfmeier & Bruelheide 2004, 2005; Buschmann, Edwards & Dietz 2005; Güsewell *et al.* 2006). A greenhouse study revealed that introduced Hawaiian and native Costa Rican populations of the tropical shrub *Clidemia hirta* displayed no significant differences in RGR, Amax or SLA (DeWalt *et al.* 2004). Common garden and greenhouse experiments showed significant but not always consistent differences in growth and reproductive characteristics between native and introduced ranges of invasive Brassicaceae species except *Bunias orientails* (Buschmann *et al.* 2005). Güsewell *et al.* (2006) found that invasive European plants produced more shoots than native American plants of *Solidago gigantea*, but they did not differ in shoot size, leaf traits and litter decomposition. A 4-month greenhouse experiment indicated that total leaf area (TLA) and SLA were significantly greater for plants from invasive populations than from native populations of *Lythrum salicaria*, but no significant differences in LAR or A were found between them (Bastlová & Kvêt 2002). Recently, a study on *Rhododendron ponticum* provided evidence for a genetic shift in invasive populations towards an increased investment in growth relative to native populations (Erfmeier & Bruelheide 2005).

Chinese tallow tree (*Sapium sebiferum* L. Roxb., Euphorbiaceae, synonyms include *Triadica sebifera*, '*Sapium*' henceforth) is native to China (Zhang & Lin 1994), and has recently become a severe invader that aggressively displaces native plants and forms monospecific stands in the south-eastern USA (Bruce *et al.* 1997). Results of recent studies on *S. sebiferum* generally support the EICA hypothesis (Siemann & Rogers 2001, 2003a,b; Rogers & Siemann 2004, 2005; Zou *et al.* 2006), suggesting that *Sapium* has evolved to be a faster-growing, less herbivore-resistant plant in response to low herbivore loads in its introduced range. In a 14-year common garden study, Siemann & Rogers (2001) found that plants of invasive Texas genotypes were larger, yet less chemically defended against herbivores than native Asia genotypes. Results of a pot experiment indicated that invasive *Sapium* genotypes tolerated simulated herbivory more effectively than native genotypes (Rogers & Siemann 2004). A common garden study showed that invasive *Sapium* populations still out-competed native populations despite more damage from herbivores in the native Chinese range (Zou, Rogers & Siemann, unpublished data). These previous studies focused primarily on a trade-off between plant growth and herbivore defence, rather than shifts in morphological and physiological traits between native and invasive populations. If the EICA hypothesis holds for *Sapium*, however, native and invasive populations may also differ in some functional traits that typically characterize invasive plant species: biomass production, total number of leaves (TLN) and leaf area (TLA), relative stem height growth rate (RHR), relative growth rate (RGR), below- and above-ground biomass allocation (RSR), non-photosynthetic and photosynthetic tissue allocation (SLA and LAR), net CO_2 assimilation (A) and dark respiration rate (R_D).

The objective of this study was to examine whether native and invasive populations of *Sapium* genetically differ in morphological and physiological traits. Specifically, we predicted that plant biomass, RGR, RHR, TLN, TLA, SLA, LAR and A would be higher, while RSR and R_D would be lower in invasive (US) than in native (Chinese) populations of *Sapium*. To test this prediction, we compared plant traits between four invasive US populations and four native Chinese populations in a greenhouse common garden experiment.

Table 1. Locations of source populations of Chinese (native) and US (invasive) *Sapium sebiferum* seeds used in the greenhouse common garden experiment

Source population	Latitude	Longitude
China		
Hefei	32°1′N	118°2′E
Chuzhou	31°36′N	117°11′E
Nanjing	32°3′N	118°50′E
Hangzhou	30°16′N	120°11′E
USA		
La Marque	29°22′N	95°3′W
Cove	29°47′N	94°46′W
Houston	29°41′N	95°24′W
Port Arthur	29°53′N	94°2′W

Materials and methods

SEEDS COLLECTION

In November and December 2004, seeds were hand collected from four populations of naturalized *Sapium* trees in Texas, USA and four populations in China (Table 1). Seeds were collected from 4 to 10 different trees of each population. Seeds from native populations were located within the northern part of *Sapium*'s range in China (Zhang & Lin 1994). Genetic analyses using microsatellites suggest that north Chinese populations are likely to be genetic candidates of *Sapium* introductions in Texas (DeWalt, Siemann & Rogers 2006; DeWalt, Siemann & Rogers, unpublished data). One thousand seeds with the similar size (weight and volume) of both native and introduced *Sapium* trees were separately planted in 65-mL cone-tainers^{TM} (Stuewe & Sons, Corvallis, OR, USA) in a greenhouse at Nanjing Agricultural University, Nanjing, Jiangsu, China (32°2′N, 118°50′E) in December 2004. Cone-tainers were filled with soil taken from the top 20 cm of the profile in fields at Jiangsu Academy of Agricultural Sciences in Nanjing where *Sapium* trees are naturalized in uncultivated areas. Planted seeds remained dormant throughout the winter season and germinated during March. The small seedlings grew in the cone-tainers for about 4 weeks until they had secondary leaves, at which time they were transplanted into pots. To minimize maternal effects due to difference in seed qualities, seedlings of similar height, basal diameter and leaf numbers (two leaves) were selected for the pot experiments in this study. Height of selected seedlings did not significantly differ between two population types at the time of transplanting ($P = 0{\cdot}17$). Difference in seedling height between two population types at the first harvest was independent of the initial height at transplanting (MANOVA, $P = 0{\cdot}24$).

POT EXPERIMENT

A 120-day greenhouse pot experiment was performed in the greenhouse at Nanjing Agricultural University, Jiangsu, China. On May 10, 2005, 48 *Sapium* seedlings of native populations (Chinese) and 48 *Sapium* seedlings of invasive populations (US) were individually transplanted into 6·50-L tree-pots filled with topsoil from the uncultivated fields. We measured stem height and recorded leaves on each seedling before transplanting. Pots were randomly placed in the greenhouse and they were reassigned haphazardly to new positions bi-weekly. To investigate seasonal dynamics of plant traits, *Sapium* seedlings were separately harvested on June 19 (40 days), July 29 (80 days) and September 7, 2005 (120 days), and the effect of population type on plant traits was separately examined within each harvest date. On each of the first two harvest dates, four seedlings per population from US and Chinese population types (2 population types × 4 populations × 4 replicates = 32 pots) were randomly selected and harvested. After each of the first two harvests, remaining pots were again randomly placed in the greenhouse and rotated bi-weekly. The final harvest consisted of the 32 seedlings not selected in either of the first two harvests. The replicate seedlings within each population were from different maternal trees. All seedlings grew healthily until the harvest.

GROWTH ANALYSES AND BIOMASS ALLOCATION

We measured plant growth and biomass allocation on each harvest date. Before harvesting, we recorded stem height and TLN per seedling. Plants were divided into roots, leaves, and stems and dried at 70 °C for 48 h. Total leaf area per seedling (TLA, cm^2) was measured on fresh leaves using a computer program SCNIMAGE (Scion Image for Windows, Scion Corporation at: www.scioncorp.com). This program is based on NIH Image that was used to calculate leaf area in our previous studies (Siemann & Rogers 2003a). Based on plant biomass and leaf area measurements, we calculated plant morphological traits: root : shoot ratio (RSR, ratio of below- to above-ground (AGB) biomass, $g\ g^{-1}$), specific leaf area (SLA; leaf area per unit leaf mass, $cm^2\ g^{-1}$), leaf area ratio (LAR; total leaf area per whole plant mass, $cm^2\ g^{-1}$). Relative stem height growth rates (RHR) were calculated as: RHR = [ln(harvest stem height) – ln(initial stem height at transplanting)]/time in growth days. Relative biomass growth rates (RGR) for each population were calculated as: RGR = [ln(seedling mass at second or third harvest) – ln(seedling mass at first or second harvest)]/interval days (40 days).

GAS EXCHANGE MEASUREMENTS

A chamber method was used to measure gas exchange rates in this study (Grogan & Chapin 2000; Maljanen *et al.* 2001; Zou *et al.* 2004). The soil–plant system CO_2 fluxes were measured in each harvest pot using a Plexiglas cylindrical 'top-hat and open-bottom'-shaped chamber fitted with a circulation fan inside (Zou *et al.* 2004, 2005, 2006). This cylindrical chamber was 25 cm diameter and 100 cm high. About 80% of ambient photosynthetic effective radiation can penetrate the transparent chambers. While taking gas samples, the chamber was placed over the vegetation with the rim of chamber fitted into the groove of pot. The top edge of each pot had a groove for filling with water to seal the rim of the gas-collecting chamber. On each date, gas samples were simultaneously taken from the headspace inside the chamber for each pot. Air temperature, humidity and photosynthetic photon flux density inside the chamber were recorded with each set of emission measurements. No significant difference in humidity inside the chambers was found before and after gas sampling. In this study, air temperature inside the chambers was 25–28 °C while measuring CO_2 fluxes on three dates. Photosynthetic photon flux density inside the chambers was about 428 μmol m^{-2} s^{-1} on June 19, 533 μmol m^{-2} s^{-1} on July 29 and 345 μmol m^{-2} s^{-1} on September 7.

Carbon dioxide mixing ratios in gas samples were detected by a modified gas chromatograph (Agilent 4890D) with a hydrogen flame ionization detector (FID) (Zou *et al.* 2005, 2006). Carbon dioxide was separated by one stainless steel column (2 m length and 2·2 mm inner diameter) packed with 50–80-mesh porapack Q. Afterwards hydrogen reduced CO_2 to CH_4 in a nickel catalytic converter at 375 °C, and CH_4 was detected by the FID. The oven was operated at 55 °C and the FID at 200 °C. Fluxes were determined from the slope of the mixing ratio changes over four consecutive 1-min intervals starting 0·5-min after chamber closure.

We measured the soil–plant system CO_2 fluxes three times on each harvest date. First, CO_2 fluxes of the soil–plant system ($FLUX_A$) were measured by transparent Plexiglas cylindrical chambers under ambient light conditions. Here, $FLUX_A$ is the measurement of the net ecosystem CO_2 exchange (NEE) between soil–plant system and atmosphere, representing the balance between C uptake by above-ground plant net photosynthesis (net CO_2 assimilation, A) and total C losses from soil respiration (S), that is, $FLUX_A = A - S$. After the transparent chambers were removed to adequately equilibrate CO_2 concentrations and temperatures with ambient conditions, the soil–plant system CO_2 fluxes were measured using the opaque chambers wrapped in a layer of sponge and aluminium foil. CO_2 fluxes measured by the opaque chambers ($FLUX_D$) stands for ecosystem respiration (ER), the sum of shoot respiration (R) and soil respiration ($FLUX_D = R + S$). Finally, a cutting-plant method was used to quantitatively partition soil respiration and shoot respiration from the whole soil–plant system CO_2 emissions. The cutting-plant method is described in detail by Zou *et al.* (2005, 2006). In this method, soil CO_2 efflux (S) measured after the shoots were removed at the soil surface is the sum of soil microbial heterotrophic respiration and root autotrophic respiration. Shoot respiration (CO_2 effluxes from shoots) was, therefore, quantified as the difference in $FLUX_D$ and S since plant photosynthesis in an opaque chamber was interrupted while gas sampling (Zou *et al.* 2004, 2005). This difference in CO_2 fluxes (mg CO_2–C m^{-2} h^{-1}) was divided by the corresponding shoot mass and then translated into shoot specific respiration rate (R_D) that was expressed in terms of a respiratory coefficient (R_D, μmol g^{-1} s^{-1}). Similarly, net CO_2 A was quantified by the difference between $FLUX_D$ and S, in terms of per unit leaf area (Aa, μmol m^{-2} s^{-1}) or leaf mass (Aw, μmol g^{-1} s^{-1}).

DATA ANALYSES

Analysis of variance (ANOVA) was used to examine the effect of the population type (native Chinese *vs* invasive US population types) and population within type on plant growth, morphological and physiological traits for each harvest time with a simple nested model. The population type was considered as fixed factor and population nested within type as random factor (Table 3). No transformations were needed if variables tended to be distributed with normality and homoscedasticity; otherwise, they were log-transformed to achieve the assumptions of ANOVA. We also checked the distribution pattern of residuals for the tests. We examined whether US and Chinese populations separated in multivariate space by conducting a discriminant analysis. Different plots in canonical components space allowed us to determine which variables contributed most to this separation, which was based on pairwise correlation coefficients between the first canonical score of discriminant ordinations and 13 variables measured on *S. sebiferum* since the variables had different units of measurement. All statistic analyses were carried out using the JMP statistical software, v. 5·1 (SAS Institute, Cary, NC, USA).

Results

PLANT GROWTH AND BIOMASS ALLOCATION

An analysis of variance (ANOVA) showed no significant difference in RHR between native Chinese and invasive US population types (Tables 2 and 3). Compared to native populations, leaf biomass (LB) of invasive populations was significantly greater over the entire experiment. During the early growth stage, root biomass (RB) of invasive populations was significantly lower than that of native populations, but no significant difference was found on July 29 and September 7, 2005. The first harvested stem (SB) and above-ground biomass (AGB) did not significantly differ between two population types, but they were significantly greater for invasive populations than for native populations at the second and third harvests. By the end of experiment, nevertheless, final harvest shoot and total biomass of invasive populations were significantly higher than those of native populations (Tables 2 and 3). The

Table 2. LS Means (± 1 SE) of morphological and physiological traits of native (Chinese) and invasive (US) populations of *Sapium sebiferum*. See text for definition of terms

	First harvest (19 June 2005)		Second harvest (29 July 2005)		Third harvest (7 September 2005)	
Variable	US†	China	US	China	US	China
RHR (mm cm^{-1} day^{-1})	0·35 ± 0·01	0·31 ± 0·02	0·21 ± 0·01	0·20 ± 0·01	0·18 ± 0·00	0·17 ± 0·00
LB (g)	1·50 ± 0·07**	1·07 ± 0·07	3·21 ± 0·17*	2·89 ± 0·15	6·47 ± 0·23***	4·68 ± 0·22
SB (g)	1·14 ± 0·04	1·14 ± 0·08	3·69 ± 0·22*	2·56 ± 0·18	6·40 ± 0·23**	5·21 ± 0·19
RB (g)	0·56 ± 0·03**	0·77 ± 0·05	1·77 ± 0·10	2·10 ± 0·13	3·20 ± 0·15	2·84 ± 0·10
AGB (g)	2·64 ± 0·11	2·22 ± 0·14	6·90 ± 0·39*	5·45 ± 0·30	12·87 ± 0·45**	9·88 ± 0·40
TB (g)	3·19 ± 0·13	2·99 ± 0·19	8·67 ± 0·49	7·55 ± 0·43	16·07 ± 0·58*	12·73 ± 0·40
TLN	31·50 ± 2·10	27·50 ± 1·70	52·50 ± 4·61	36·71 ± 4·12	70·21 ± 4·02	63·81 ± 6·23
TLA (cm^2)	62·40 ± 2·50*	51·00 ± 3·20	127·50 ± 7·22**	91·22 ± 4·63	155·13 ± 5·81**	107·42 ± 4·93
RSR (g g^{-1})	0·21 ± 0·01***	0·35 ± 0·02	0·26 ± 0·01**	0·39 ± 0·02	0·25 ± 0·01	0·29 ± 0·01
SLA (m^2 g^{-1})	41·78 ± 1·50	41·61 ± 1·92	39·66 ± 2·21***	31·87 ± 1·62	24·10 ± 1·00	20·35 ± 0·65
LAR (m^2 g^{-1})	19·58 ± 0·67*	16·91 ± 1·07	14·73 ± 0·83**	12·25 ± 0·61	9·71 ± 0·41	8·14 ± 0·30
Aa (μmol m^{-2} s^{-1})	21·94 ± 0·74**	16·48 ± 1·18	25·58 ± 1·86*	18·33 ± 0·97	19·15 ± 0·64*	14·39 ± 0·67
Aw (μmol g^{-1} s^{-1})	91·58 ± 3·20	77·72 ± 5·31	95·22 ± 5·46***	60·91 ± 3·21	46·02 ± 1·78**	32·16 ± 1·03
R_D (μmol g^{-1} s^{-1})	21·24 ± 0·96	21·09 ± 1·65	10·82 ± 0·91	10·22 ± 0·76	9·77 ± 0·40	10·21 ± 0·38
RGR (mg g^{-1} day^{-1})	–	–	25·03 ± 0·60*	23·19 ± 0·45	15·47 ± 0·21*	13·04 ± 0·82

†Significance difference in traits between native and invasive population types: **P* < 0·05, ***P* < 0·01, ****P* < 0·001. *F*-values and significance levels of ANOVAs testing for effects of population type (native Chinese *vs* invasive US populations) and population within type on plant traits are listed in Table 3.

Table 3. ANOVAs for difference in traits between invasive and native population types (source range, df = 1,6) of *Sapium sebiferum* and among populations within the type (df = 6,24). See text for definition of terms

		First harvest		Second harvest		Third harvest	
Variable	Source	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
RHR	Population type	5·9	0·05	1·1	0·34	3·8	0·10
	population	0·6	0·72	0·1	0·99	0·9	0·53
LB	Population type	18·9	0·005	7·0	0·04	19·3	< 0·001
	Population	1·1	0·39	0·3	0·94	1·8	0·13
SB	Population type	0·0	0·95	13·1	0·01	21·5	0·004
	Population	1·3	0·30	1·5	0·22	0·4	0·63
RB	Population type	24·8	0·003	2·8	0·14	2·1	0·20
	Population	0·6	0·76	1·7	0·15	2·5	0·06
AGB	Population type	6·1	0·05	18·3	0·01	22·7	0·003
	Population	0·9	0·51	0·5	0·81	1·1	0·39
TB	Population type	0·9	0·37	4·8	0·07	17·0	0·01
	Population	0·8	0·57	0·6	0·70	1·2	0·36
TLN	Population type	1·0	0·36	2·2	0·19	0·4	0·54
	Population	3·4	0·01	8·5	< 0·001	7·4	< 0·001
TLA	Population type	7·6	0·03	44·5	0·001	35·9	0·001
	Population	1·0	0·43	0·4	0·87	1·1	0·37
RSR	Population type	159·5	< 0·0001	26·2	0·002	4·9	0·07
	Population	0·2	0·98	1·1	0·41	1·8	0·14
SLA	Population type	0·0	0·91	57·8	< 0·001	6·1	0·05
	Population	0·3	0·93	0·1	0·99	1·9	0·12
LAR	Population type	11·6	0·01	26·8	0·002	5·0	0·07
	Population	0·3	0·91	0·2	0·97	2·5	0·05
Aa	Population type	19·6	0·004	13·6	0·01	15·7	0·01
	Population	0·7	0·62	1·1	0·41	2·0	0·10
Aw	Population type	5·7	0·06	129·7	< 0·001	35·2	0·001
	Population	0·9	0·54	0·2	0·97	1·4	0·26
R_D	Population type	0·0	0·95	0·1	0·76	0·3	0·59
	Population	1·8	0·14	4·8	0·002	2·7	0·04

calculated biomass RGR were significantly greater for invasive US populations than for native Chinese populations (Table 2, $F_{1,6}$ = 6·17, *P* < 0·05 on July 29, 2005, $F_{1,6}$ = 8·31, *P* < 0·05 on September 7, 2005). In contrast, no significant difference in growth among populations within each type (native Chinese or invasive US population type) was found on RHR, LB, SB, AGB and TB throughout the experiment (Table 3).

Total number of leaves (TLN) per seedling did not significantly differ between native and invasive population types, but it significantly differed among populations within each type (Tables 2 and 3). In contrast, TLA per seedling of invasive populations was significantly greater than that of native populations. Also, LAR were significantly higher for invasive populations than for native populations on June 19 and July 29, and tended to be greater on September 7 (Tables 2 and 3). Significant differences in SLA and RSR between native and invasive population types were found on June 19 and July 29, but they did not differ among populations within each type (Tables 2 and 3).

GAS EXCHANGE

Net CO_2 A in terms of leaf area (Aa) or leaf mass (Aw) was significantly greater for invasive populations than for native populations under the photosynthetic photon flux density 330–550 $\mu mol\ m^{-2}\ s^{-1}$ in this study (Tables 2 and 3). In contrast, R_D did not differ between native and invasive populations throughout the experiment, while a significant variation among populations within each type was found on July 29 and September 7, 2005.

DISCRIMINANT ANALYSIS

The canonicals of discriminant analyses of 13 morphological and physiological traits provided a clear separation of US and Chinese population types throughout the experiment. For analyses on three different dates, the first two axes explained 69%–77% of the total variation (Fig. 1). Pairwise correlation analyses showed that RSR was the variable most strongly correlated with the first canonical during the early growth stage (Table 4), which supported the univariate analyses showing that invasive population types had significantly lower RSR than native population types on June 19 (Tables 2 and 3). At the end of experiment, however, Aa (Aw) and TLA became the physiological and morphological trait variables that were most strongly correlated with the first canonical. This suggests that Aa and TLA accounted for distinguishing invasive population types from native population types of *Sapium* (Table 4). Over the entire experiment, pairwise correlation coefficients between the first two canonical scores of discriminant ordinations and 13 variables suggested that RSR, TLA and A were the functional traits that contributed most to the distinction between population types from native and invasive ranges (Table 4).

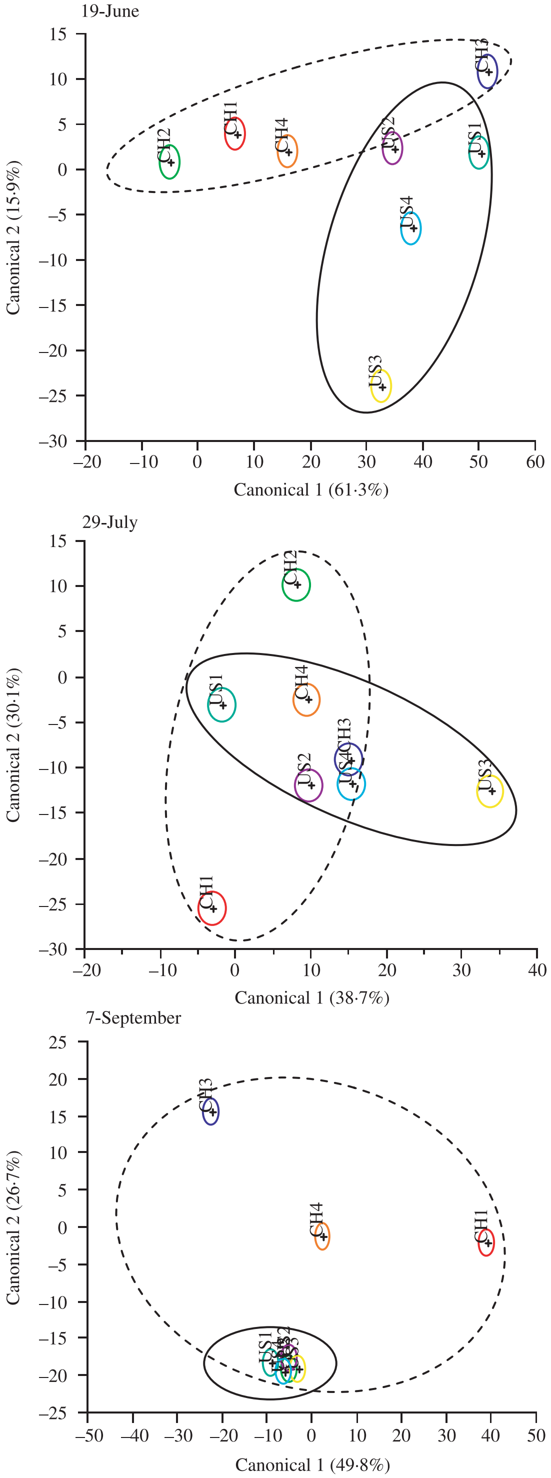

Fig. 1. Plots for discriminant analysis ordination of four invasive US and four native Chinese populations based on morphological and physiological traits shown in Tables 2 and 3. US1, US2, US3 and US4 are four invasive US populations, and CH1, CH2, CH3 and CH4 represent four native Chinese populations.

Discussion

SHIFTS IN FUNCTIONAL TRAITS

One of the most important findings of this study was that shifts in morphological and physiological traits might combine to result in different growth strategies for native *vs* invasive populations of *Sapium*. Most individual traits of invasive US populations of *Sapium* differed from native Chinese populations. Shifts in the individual traits may work in combination to determine alternative adaptive strategies of invasive populations

Table 4. Pairwise correlation coefficients between the first and second canonical scores of discriminant ordinations shown in Fig. 1 and 13 variables measured on *Sapium sebiferum* at different days in a greenhouse common garden experiment. The largest correlation coefficients are shown in bold. See text for definition of terms

	First harvest		Second harvest		Third harvest	
Variable	Canonical 1	Canonical 2	Canonical 1	Canonical 2	Canonical 1	Canonical 2
RHR	0·304	–0·116	0·171	0·051	0·124	–0·301
LB	0·465**	–0·369*	0·083	–0·206	–0·187	–0·729***
SB	0·146	0·104	0·239	–0·117	–0·294	–0·523**
RB	–0·391*	0·311	–0·030	–0·325	–0·202	–0·347
AGB	0·260	–0·185	0·362	–0·160	–0·238	–0·648***
TB	0·102	–0·062	0·289	–0·220	-0·237	–0·606***
TLN	0·160	0·069	0·343	–0·227	0·117	–0·350*
TLA	0·412*	–0·104	0·070	**0·500****	**0·466****	0·308
RSR	**–0·508****	0·370*	**–0·604*****	–0·326	–0·386*	–0·423*
SLA	0·146	0·165	0·297	–0·085	–0·097	–0·228
LAR	0·374*	–0·057	0·102	–0·043	–0·270	–0·127
Aa	0·195	**–0·373***	0·096	–0·136	0·070	**–0·748*****
Aw	0·276	–0·093	0·515**	–0·015	–0·099	–0·534**
R_D	–0·126	–0·149	–0·306	–0·164	0·397*	–0·140

*P < 0·05, **P < 0·01, ***P < 0·001.

relative to native populations of *Sapium*. For instance, lower RSR suggests that invasive population types used soil nutrients more efficiently compared to native population types, and thus can uptake higher nutrients with relatively lower below-ground C allocation. By virtue of their higher TLA and A, invasive populations apparently capture and use light more efficiently than native populations. Thus, the suite of morphological and physiological traits functioning together may result in different growth strategies between native and invasive populations of *Sapium*.

Genetic changes among conspecifics in their native and introduced ranges account for differences in plant functional traits observed between native and invasive population types (Growth-Differentiation Balance (GDB) hypothesis, Herms & Mattson 1992; EICA hypothesis, Blossey & Nötzold 1995). From these genetic-shift hypotheses, we predict that introduced US populations of *Sapium* would have greater TLA, SLA, LAR and A, but lower RSR and R_D than native Chinese populations because such characteristics have been predicted to be associated with fast-growing (growth-dominated) rather than slow-growing (differentiation-dominated) population types (Herms & Mattson 1992). Measurements of most morphological and physiological traits are generally consistent with our prediction, except for no significant difference in RHR, TLN and R_D throughout the experiment. Such genetic shifts in morphological and physiological traits were also partially found on *L. salicaria* (Bastlová & Květ 2002), *R. ponticum* (Erfmeier & Bruelheide 2004, 2005), *Barbarea vulgaris* and *Rorippa austriace* (Buschmann *et al.* 2005) as well as *S. gigantea* (Güsewell *et al.* 2006), when native and invasive populations were compared in a common garden study.

One mechanism by which invasive plants may achieve fast-growth is through changes in below- and above-ground biomass allocation (Schierenbeck, Mack & Sharitz 1994; Gremmen, Chown & Marshall 1998; Sexton, McKay & Sala 2002; Wilsey & Polley 2006). Based on a review of the previous studies that compared the root : shoot ratio of exotic plants and the native plants that they displace, Ehrenfeld (2003) proposed that lower RSR is closely associated with the increased size and growth rate of invasive plants. This hypothesis is supported by the result of Wilsey & Polley (2006) who showed that RSRs of introduced grasses were lower than those of native grasses when they were grown in a common environmental condition. In the present study, we found that RSRs were significantly lower for invasive populations compared to native populations of *Sapium*, which is consistent with the result of our previous common garden study (Zou *et al.* 2006).

Lower RSR of invasive populations relative to native populations may reflect a genetic shift as an evolutionary response to the absence of natural enemies in the introduced range. Some studies have suggested that herbivory pressure has significant impacts on biomass allocation between below- and above-ground (Strauss & Agrawal 1999; Gassmann 2004). Higher RSRs are often found to be associated with greater shoot herbivory damage for invasive plants (Herms & Mattson 1992; Jeschke, Baig & Hilpert 1997; Shen *et al.* 2005). In this context, invasive populations evolved under less herbivory in the introduced range would be predicted to have lower RSR than native populations evolved under heavier herbivore pressure in the original range. This genetic shift suggests that relatively more mass was allocated to photosynthetic tissues for the invasive populations, but more mass to the root growth for the native populations.

Leaf traits have been well documented to be one of the most important characteristics of vigorously growing invasive plants (e.g. Pattison *et al.* 1998; Baruch & Goldstein 1999; Durand & Goldstein 2001; Smith & Knapp 2001; Grotkopp *et al.* 2002; McDowell 2002). Plant photosynthesis depends largely on TLA. Specific leaf area (SLA) or LAR as indicators of photosynthetic surface area per unit investment in leaf tissue or in whole plant are often positively associated with rapid growth rates. Several previous common garden studies have found differences in leaf traits between native and invasive populations of introduced plants. Although no significant differences in leaf traits were found by DeWalt *et al.* (2004) and Güsewell *et al.* (2006), for example, a 4-month greenhouse common garden experiment indicated that TLA and SLA were significantly greater for plants from invasive populations than native populations of *L. salicaria* (Bastlová & Květ 2002). In the present study, we also found that TLA, SLA and LAR of invasive populations were generally greater than those of native populations, which suggests that invasive *Sapium* plants in the introduced range have developed a strategy that minimizes carbon costs associated with photosynthesis, making more carbon available for tissue growth.

Another possible mechanism contributing to invasive plant success is through increasing net CO_2 A. It is well documented that some invasive plants outperformed the co-occurring native species through maximizing photosynthesis (e.g. Baruch & Goldstein 1999; Durand & Goldstein 2001; McDowell 2002; Nagel & Griffin 2004). Although no significant difference in net CO_2 A between native and invasive populations was found for the invasive tropical shrub *C. hirta* (DeWalt *et al.* 2004) or *L. salicaria* (Bastlová & Květ 2002), greater net CO_2 A of invasive populations relative to native populations of *Sapium* found in this study suggests that maximizing photosynthesis might evolve as a strategy that contributes to the success of invasive plants in the introduced range. Contrary to the prediction, we found no significant difference in R_D between two population types of *Sapium* over the whole season. Since dark respiration is often used to estimate plant tissue construction, greater A but no difference in R_D suggest that at a similar cost, invasive populations were able to gain higher photosynthetic rates, which contributed to their higher growth rates than native population types.

The discriminant analysis summarizes plant variable measurements from this study. The morphological and physiological traits measured in this study proved to be powerful in discriminating between invasive and native population types of *Sapium* (Fig. 1), and, therefore, may be important factors contributing to its invasive success in the introduced range. In particular, RSR, TLA and A were identified as the three most powerful functional traits in the discriminant analysis. Lower RSR is supported by the result of a previous 4-month pot experiment indicating that higher soil nitrogen availability and soil nitrogen uptake by plants were associated with invasive populations rather than native populations of *Sapium* (Zou *et al.* 2006). Higher TLA and A would give invasive populations an advantage over native populations in the use of light resources. As a result, the combination of lower RSR and higher A, and TLA may have important implications for their invasive success in the introduced range.

DIFFERENCE IN GROWTH

It is not surprising that some plant variables (SB, TB and SLA) measured at the first harvest did not significantly differ between native and invasive population types since this experiment was initiated using seedlings of similar size. However, differences in plant variables between native and invasive populations became more apparent over time (Tables 2 and 3). Indeed, final harvest shoot mass (AGB) and total mass (TB) of the invasive US populations of *Sapium* were significantly greater than those of the native Chinese populations by the end of the experiment, although some growth variables such as RHR and TLN did not significantly differ. Moreover, RGRs were significantly higher for invasive populations than for native populations. Together with the previous studies indicating the higher growth rate of invasive populations relative to native populations of *Sapium* (Siemann & Rogers 2001, 2003a,b; Rogers & Siemann 2004, 2005; Zou *et al.* 2006), the results of this study are generally in support of the EICA hypothesis suggesting that *Sapium* has evolved to be a fast-growing plant in response to the absence of herbivores in the introduced range.

Local maladaptation (e.g. to specific attack by soil pathogens to native Chinese populations) due to non-sterilized soil from the native range used in this study could have contributed to growth differences between two population types. However, this speculation is not supported for two reasons. First, we did not find any obvious root damage over the entire experiment. On the contrary, all seedlings grew healthily until the harvest. Second, the EICA hypothesis proposes that invasive populations would be more frequently attacked than native populations because they are expected to be less well defended against soil pathogens. Indeed, the results of this study strongly suggest that the growth differences between two population types of *Sapium* were largely due to genetic shifts in ecological and morphological traits rather than differential attacks by soil pathogens.

Although the expression of many plant traits is environment dependent, and the performance of invasive species relative to native species, or invasive populations relative to native populations of introduced plants, can differ with environments (Schweitzer & Larson 1999; Daehler 2003; DeWalt *et al.* 2004; Burns 2006), we did not examine plant traits under various environmental conditions in this study. However, invasive *Sapium* plants have showed greater performance when they were compared with native tree species under different soil nutrients, water regimes and light conditions (Rogers & Siemann 2002; Siemann & Rogers 2003c; Butterfield, Rogers & Siemann 2004). Some previous studies on *Sapium* indicated that greater performance and competitive ability of invasive populations relative to native populations were independent of soil nutrients (Zou *et al.* 2006, Zou, Rogers & Siemann, unpublished data). Lower RSR of invasive populations relative to native populations of *Sapium* and no significant difference in R_D in this study were consistent with a previous comparative study, but they were also found to be independent of soil resource levels (Zou *et al.* 2006). This suggests that other genetic shifts in morphological and physiological traits found in this study may also be independent of environmental conditions.

In the past decade, a number of studies have attempted to test the EICA hypothesis, and they have produced inconsistent results (Daehler & Strong 1997; Willis & Blossey 1999; Willis, Memmott & Forrester 2000; Thebaud & Simberloff 2001; Bossdorf *et al.* 2005). In these EICA studies, some approaches have been used, such as examining phenotypic plasticity across different environments, genetic analysis, or comparing performance of native and invasive populations in a common garden (Bossdorf *et al.* 2005). Although few studies have concentrated on changes in plant morphological and physiological traits between native and invasive populations of introduced plants, investigation of shifts in plant functional traits may provide better insights into strategies that invasive plants use to achieve their fast growing rates. Thus, it could also be an effective approach for testing the EICA hypothesis and may increase our understanding of invasion mechanisms and the invasion process.

Acknowledgments

We thank Yao Huang, Lianggang Zong, Yanyu Lu and Shutao Chen for their help in collecting seeds and taking emission samples; two anonymous referees for helpful comments on the manuscript; Nanjing Agricultural University for use of greenhouse and laboratory space; and the US National Science Foundation (DEB-0315796) for support.

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Received 14 February 2007; revision 29 March 2007; accepted 27 April 2007
Editor: James Cresswell