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Plasticity of *Sapium sebiferum* seedling growth to light and water resources: Inter- and intraspecific comparisons

Jianwen Zou[a,b,*], William E. Rogers[a,c], Evan Siemann[a]

[a]*Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77005, USA*
[b]*College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing 210095, China*
[c]*Department of Rangeland Ecology and Management, Texas A&M University, College Station, TX 77843, USA*

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Abstract

Two main hypotheses have been posed to explain the role of phenotypic plasticity in the invasive success of exotic plants: (1) invasive species may be more plastic than resident species in the introduced range, and (2) invasive populations of an exotic species may be more plastic relative to native populations due to evolutionary changes after introduction. To test the first hypothesis, we conducted a greenhouse pot experiment in which seedlings of invasive *Sapium sebiferum* competed against native *Schizachyrium scoparium* grasses under different light and water conditions. To test the second hypothesis, we performed an additional greenhouse pot experiment in which seedlings from native and invasive populations of *S. sebiferum* were grown under environmental treatments analogous to those in the first greenhouse experiment. Compared to native *S. scoparium* grasses, or to *S. sebiferum* seedlings from native populations, growth rates of *S. sebiferum* seedlings from invasive populations were generally higher. When they were competing with *S. scoparium* grasses, the greater response of *S. sebiferum* to light and water conditions reflected different patterns: *S. sebiferum* seedlings were better able to respond with increased growth in unflooded soils, whereas *S. sebiferum* had more robust growth in the shaded conditions. No difference in responses to change in water conditions, but a significant difference in responses to variation in light conditions was found between two population types of *S. sebiferum*. The results of this study suggest that relative to *S. scoparium*, the greater plasticity of *S. sebiferum* to variation in light conditions is evolved in the introduced range, while that to variation in water conditions reflects an innate property.

Zusammenfassung

Zwei Haupthypothesen wurden aufgestellt, um die Rolle der phänotypischen Plastizität für den Einwanderungserfolg von exotischen Pflanzen zu erklären: (1) Invasive Arten könnten plastischer sein als einheimische Arten im Einwanderungsgebiet. (2) Aufgrund von evolutiven Änderungen nach der Einschleppung könnten die invasiven Populationen einer exotischen Art plastischer sein als Populationen im Ursprungsgebiet.

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[*]Corresponding author at: College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing 210095, China. Tel.: +86 25 84396286; fax: +86 25 84396406.
E-mail addresses: jwzou21@njau.edu.cn, jwzou@rice.edu (J. Zou).

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Um die erste Hypothese zu testen, führten wir ein Gewächshausexperiment durch, bei dem Keimlinge der invasiven Art *Sapium sebiferum* mit dem indigenen Gras *Schizachyrium scoparium* unter verschiedenen Licht und Feuchtebedingungen konkurrierten. Um die zweite Hypothese zu testen, führten wir ein weiteres Gewächshausexperiment durch, bei dem Keimlinge von indigenen und invasiven Populationen von *S. sebiferum* unter dem ersten Experiment analogen Bedingungen wuchsen.

Verglichen mit dem indigenen Gras *S. scoparium* oder Keimlingen aus indigenen *S. sebiferum*-Populationen waren die Wachstumsraten von *S. sebiferum*-Keimlingen aus invasiven Populationen im allgemeinen höher. Bei der Konkurrenz mit *S. scoparium*-Gras ließ die stärkere Antwort von *S. sebiferum* auf Licht- und Feuchtebedingungen verschiedene Muster erkennen: *S. sebiferum*-Keimlinge waren besser befähigt, mit stärkerem Wachstum in nicht geflutetem Boden zu reagieren, während *S. sebiferum* kräftigeres Wachstum unter Schattbedingungen aufwies. Kein Unterschied in der Reaktion auf geänderte Feuchtebedingungen aber ein signifikanter Unterschied in der Reaktion auf variierte Lichtbedingungen bestand zwischen den beiden Popualtionstypen von *S. sebiferum*.

Die Ergebnisse dieser Studie legen nahe, daß verglichen mit *S. scoparium* bei *S. sebiferum* eine größere Plastizität gegenüber variierten Lichtbedingungen ausgebildet ist, während die Plastizität gegenüber Wasserbedingungen eine angeborene Eigenschaft darstellt.

Keywords: Invasive species; Phenotypic plasticity; Post-introduction evolution; Pre-adaptation; Reaction norm; Resources

Introduction

One explanation for the invasive success of exotic plants in the introduced range is that they can use resources more efficiently than the resident plant species (Davis, Grime, & Thompson 2000; Tilman 1999). The pre-adaptation hypothesis attributes the successful invasion of exotic plants to their innate traits pre-adapted in the native ranges. This hypothesis posits that some invaders are innately better competitors because they have evolved in a more competitive environment. Once established in the introduced range, thus, invasive plants may gain a systematic advantage over competitively inferior native plants.

Higher resource use efficiency of invasive plants may also be achieved due to evolutionary changes in the introduced range. For instance, the evolution of increased competitive ability (EICA) hypothesis proposes that as a response to escape from natural enemies, natural selection favors invasive plants evolving traits associated with rapid growth, thereby enhancing resource acquisition, and eventually increasing their population abundance (Blossey & Nötzold 1995; Zou, Rogers, DeWalt, & Siemann 2006).

Higher resource use efficiency of invasive plants may allow greater phenotypic plasticity. Phenotypic plasticity is the property of a genotype to express different phenotypes in different environments. Some studies suggest that phenotypic plasticity plays an important role in the invasive success of exotic plants (Baker 1965; Rice & Mack 1991; Richards, Bossdorf, Muth, Gurevitch, & Pigliucci 2006). Corresponding to the pre-adaptation versus post-introduction evolution scenarios, recent studies on phenotypic plasticity in the context of plant invasions have posed two distinct hypotheses: (1) plasticity is one characteristic of an "ideal weed" and thus invasive species may be more plastic than non-invasive or native ones (the "general-purpose genotype" of Baker (1965)); (2) invasive populations of an exotic species may have greater plasticity relative to native populations due to evolutionary changes in the introduced range (Richards et al. 2006). If genetic variation in plasticity occurs in invasive plants, and these genetic variations give rise to their higher fitness in the novel environment, evolution of increased plasticity would be expected. Consequently, rapid evolution of plasticity would contribute to their invasion success in the introduced range (Agrawal 2001; Donohue, Pyle, Messiqua, Heschel, & Schmitt 2001; Yeh & Price 2004).

Clearly, these two hypotheses focus on phenotypic plasticity of invasive plants at different levels. The first hypothesis is usually addressed with cross-species comparisons (Leishman & Thomson 2005; Williams & Black 1994), while the second uses ecological genetic approaches to make intraspecific comparisons within a specific invasive species (DeWalt, Denslow, & Hamrick 2004; Kaufman & Smouse 2001). Although the role of phenotypic plasticity in plant invasions has been widely explored by comparing invasive species with other species, these interspecific comparisons do not address whether advantageous plasticity of an invasive plant species reflects pre-adaptation in its native range, or is evolved after introduction in the novel range. To address this, intraspecific comparison of native and invasive populations of an invasive plant species is necessary (DeWalt et al. 2004; Kaufman & Smouse 2001). To our knowledge, no study has simultaneously examined phenotypic plasticity of invasive plants at these two different ecological levels.

Chinese tallow tree (*Sapium sebiferum* L. Roxb., Euphorbiaceae) is native to China, where it is naturally occurring and cultivated for 14 centuries (Zhang & Lin 1994). *S. sebiferum* was introduced in the USA in 1772 and is naturalized throughout the southeastern USA from the Gulf Coast of Texas to the coast of North Carolina (Bruce, Cameron, Harcombe, & Jubinsky 1997). In coastal Texas, much of the grassland formerly dominated by little bluestem (*Schizachyrium scoparium* Michx.) has been converted to *S. sebiferum* forests. The rapid switch from grassland to *S. sebiferum* forest suggests some positive feedback mechanisms, including high local seed input (Scholes & Archer 1997; Siemann & Rogers 2006) and changes in resources that favor *S. sebiferum* seedlings in competition with grasses (Siemann & Rogers 2003a). *S. sebiferum*'s success may also be due to phenotypic plasticity that allows *S. sebiferum* to have an advantage over native trees and resident grasses in a broader range of environments (Rogers & Siemann 2002, 2003).

Some studies suggest that invasive *S. sebiferum* has become a faster growing plant relative to conspecifics from the native range due to a genetic trade-off between growth and defense (e.g., Siemann & Rogers 2001, 2003b; Zou et al. 2006). In previous studies, lower root to shoot ratio, greater leaf area and higher net CO_2 assimilation were found to be associated with invasive populations of *S. sebiferum* (Zou et al. 2006; Zou, Rogers, & Siemann 2007). It has been shown that invasive populations can accelerate soil carbon and nitrogen processes, and use soil nutrients more efficiently than native populations of *S. sebiferum* (Zou et al. 2006). These shifts in ecological and morphological traits may be the result of a difference in plasticity between native and invasive populations of *S. sebiferum*.

Here, we conducted two separate greenhouse experiments to address phenotypic plasticity of *S. sebiferum* by inter- and intraspecific comparisons. To test whether invasive *S. sebiferum* plants have greater plasticity relative to resident *S. scoparium* grasses, we conducted an experiment ("interspecific experiment") in which invasive *S. sebiferum* seedlings competed with resident *S. scoparium* grasses under various light and water environments. To examine whether the plasticity of *S. sebiferum* is pre-adapted in its native range or evolved in the introduced range, we performed an experiment ("intraspecific experiment") to examine the differences in phenotypic plasticity between native and invasive populations of *S. sebiferum*. We predicted that (1) the plasticity of growth to light and water environments would be greater for *S. sebiferum* than for *S. scoparium* when they were grown together, and (2) relative to native populations, invasive populations of *S. sebiferum* would have higher plasticity of growth traits to light and water environments.

Material and methods

Interspecific experiment

Soil, *S. sebiferum* seeds and *S. scoparium* clumps were all collected at the University of Houston Coastal Center, a research area located ~50 km south-east of Houston, TX, USA. The climate is semitropical with typical rainfall of 120 cm and a growing season of 250 days. Soils are Lake Charles Clay (fine, montmorillonitic, thermic Typic Pelludert), with a clay content of 40–60%. The annually mowed and occasionally flooded coastal grassland areas are dominated by grasses (75% of mass) with *S. scoparium* as the main species (34% of cover; Harcombe, Cameron, & Glumac 1993). Forbs comprise about 18% of the plant cover. In unmowed parts of the Coastal Center, the typical cover is *S. sebiferum* forests. We collected the soil and the *S. scoparium* clumps in September 1998. *S. sebiferum* seeds were collected from trees in October and November 1998 and stored at room temperature.

In September 1998, we transplanted 40 clonal bunches of *S. scoparium* from coastal grassland into 9-L pots in an unheated greenhouse. After they senesced in January, we clipped the senesced vegetation to a height of 2.5 cm above ground level. Following a month of regrowth, we planted one newly sprouted *S. sebiferum* seed into the middle of each *S. scoparium* bunch. Once all 40 *S. sebiferum* seedlings had initiated their primary leaves, we implemented our treatments. The two treatments were soil water regime (flooded versus unflooded) and light (85% shade versus ambient light) assigned in a complete factorial, randomized design with 10 replicates. Plants in the shaded treatment were placed under a black polypropylene shade cloth that intercepted 87% of photosynthetically active radiation as measured by weekly midday readings with a Decagon Accupar linear PAR ceptometer (Decagon Devices, Pullmann, WA, USA). Plants in the unshaded treatments received ambient light. Because there may have been differences in light or temperature in different positions within the greenhouse, we rotated the plants within each shade treatment frequently. The pots in the flooded treatment were each placed inside a 12-L bucket. The water was ~1 cm above the soil surface. Pots were watered daily and rotated frequently. Two *S. sebiferum* seedlings died in the light-unflooded treatment.

At the end of the 15th week, we harvested *S. sebiferum* and *S. scoparium* biomass. We gently washed *S. sebiferum* and *S. scoparium* roots from the soil and dried and weighed below- and aboveground biomass separately. Because the fibrous *S. scoparium* roots can be distinguished from the stout *S. sebiferum* tap root, we had separate root masses for each species in addition to aboveground data for each.

Intraspecific experiment

In November and December 2004, seeds were hand collected from five populations of naturalized *S. sebiferum* trees in the invasive North American range and five populations in the native Chinese range (see Appendix A). Seeds were collected from multiple trees of each population. Seeds of similar size (weight and volume) of both native and introduced *S. sebiferum* 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 2005. 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, China, where *S. sebiferum* trees are naturalized in uncultivated areas. Planted seeds remained dormant throughout the winter season and germinated during March. To minimize maternal effects due to differences 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 the two population types at the time of transplanting ($P = 0.21$). The difference in seedling height between two population types at the harvest was independent of the initial height at transplanting (MANOVA, $P = 0.36$).

A 120-day pot experiment was performed in an unheated greenhouse at Nanjing Agricultural University. The experimental soil was classified as hydromorphic, consisting of 29% sand, 16% silt and 55% clay with an initial $pH_{(H_2O)}$ of 6.7. The light and water treatments in this experiment were comparable to those in the interspecific experiment, but the two experiments used different local soils and represented a different competition setting. In the intraspecific experiment, 160 seedlings from native and introduced ranges were planted in a four-factorial random design (light × water × population type × population $= 2 \times 2 \times 2 \times 5$) with four replicates. On May 15, 80 *S. sebiferum* seedlings of native populations (Chinese) and 80 *S. sebiferum* seedlings of invasive populations (US) were individually transplanted into 6.5-L pots filled with topsoil from the uncultivated fields and assigned to the ambient light and shaded treatments. Within each light treatment, pots were randomly placed in the greenhouse and rotated weekly independent of population type and water treatments. In the flooded treatment, the pots were watered daily and remained at ~1 cm water level. We measured stem height and recorded leaves on each seedling before transplanting. All seedlings survived until the harvest.

We recorded stem height and total number of leaves per seedling before transplanting and harvest. Harvested shoots were divided into leaves and stems and separately dried and weighted. Total leaf area per seedling (TLA, cm^2) was measured on fresh leaves using the computer program ScnImage (Scion Image for Windows, Scion Corporation at: www.scioncorp.com). This program is based on NIH Image (Siemann & Rogers 2003b). Relative stem height growth rates (RHR) were calculated as follows: RHR = (harvest stem height−initial stem height at transplanting)/initial height/time in growth days.

Data analyses

To compare plant growth and plasticity of *S. sebiferum* versus *S. scoparium* in the interspecific experiment, the harvested biomass of each species of different treatments was normalized to that of the flooded–shaded treatment for each species (i.e., the average for flooded–shaded was equal to one). Normalized variables were used to examine the effects of light, water regime, species and their interactions on plant growth with a three-way ANOVA. The differences in plasticity to light and water between two species were depicted by the reaction norm that was statistically represented by the significance in interactions of environmental factor (light or water) with species. The normalized biomass of root, leaf, shoot and total was square-root transformed to achieve the assumptions of ANOVA.

In contrast to the focus on two different species in the interspecific experiment, the intraspecific experiment focused on differences in growth of invasive versus native populations of *S. sebiferum*. Thus, we conducted an ANOVA to examine the effects of light, water, origin of populations (native versus invasive population types) and population as well as their interactions on growth variables of *S. sebiferum* seedlings. The effects of light, water and origin were treated as fixed factors, and population nested within origin as random factor. To achieve normality and homoscedasticity, TLA was square-root transformed and leaf and shoot biomass were cube-root transformed for tests. Similarly, the differences in plasticity between two population types were depicted by the reaction norm under different environments and statistically represented by the significance in interactions of origin with environmental factors. All statistical analyses were carried out using JMP, version 5.1 (SAS Institute, Cary, NC, USA).

Results

In the interspecific experiment, no significant interaction of species with light or water regime suggested similar responses of root growth to various light and water environments for both species (Table 1, Fig. 1). Root growth was not significantly affected by water

Table 1. ANOVAs for the effects of shading (L, 15% ambient light) and flooding (W) on relative growth of invasive *Sapium sebiferum* seedlings and native *Schizachyrium scoparium* grasses

Source	d.f.	Root biomass			Leaf biomass			Shoot biomass			Total biomass		
		SS	*F*	*P*	*SS*	*F*	*P*	*SS*	*F*	*P*	*SS*	*F*	*P*
L	1	0.509	10.32	**0.002**	0.089	1.11	0.30	0.001	0.04	0.84	0.037	0.77	0.38
W	1	0.146	2.96	0.09	3.449	42.84	<**0.0001**	0.845	26.70	<**0.0001**	0.883	18.28	<**0.0001**
Species	1	0.430	8.72	**0.004**	3.999	49.67	<**0.0001**	4.513	142.62	<**0.0001**	2.121	43.93	<**0.0001**
L × W	1	0.058	1.18	0.28	0.177	2.20	0.14	0.056	1.76	0.19	0.022	0.45	0.51
L × species	1	0.001	0.02	0.88	1.152	14.31	<**0.001**	0.267	8.45	**0.005**	0.253	5.23	**0.03**
W × species	1	0.003	0.06	0.81	1.060	13.16	<**0.001**	0.148	4.67	**0.03**	0.218	4.51	**0.04**
W × L × species	1	0.000	0.00	1.00	0.177	2.28	0.14	0.122	3.86	**0.05**	0.130	2.68	0.11
Model	7	1.068	3.09	**0.007**	10.238	18.17	<**0.0001**	6.000	27.09	<**0.0001**	3.666	10.85	<**0.0001**
Error	70	3.453	5.636	2.215	3.379								

regimes for either *S. sebiferum* or *S. scoparium*. Compared to ambient light conditions, in contrast, root growth of both species was significantly decreased by shading (Table 1, Fig. 1). Relative to flooded treatments, leaf, shoot and total biomass of *S. sebiferum* seedlings were significantly higher when they grew in the unflooded soils. Shading significantly increased shoot and total biomass of *S. sebiferum* seedlings compared to ambient light conditions. Leaf, shoot and total biomass of *S. scoparium* plants were not significantly affected by soil water status or light availabilities (Fig. 1). In general, the relative growth rate of *S. scoparium* was slower than that of *S. sebiferum* when they were competing against each other, particularly in unflooded soils or under shaded conditions. A significant interaction of light or water with species for relative leaf, shoot and total biomass suggests greater plasticity of *S. sebiferum* growth to water or light than that of *S. scoparium* (Table 1, Fig. 1).

Seedling growth was higher in unflooded soils than in flooded conditions for both native and invasive populations of *S. sebiferum* in the intraspecific experiment (Table 2, Fig. 2). Compared to ambient light treatments, seedling growth of native and invasive populations of *S. sebiferum* was significantly decreased by shading (Table 2, Fig. 2). Height growth rate was significantly higher for invasive populations relative to native populations of *S. sebiferum*, which was independent of water and light conditions (Table 2, Fig. 2). Total leaves per seedling did not significantly differ between two population types (Table 2), but leaf area, leaf biomass and shoot biomass were generally higher for invasive populations than for native populations of *S. sebiferum* (Table 2), particularly when they grew under ambient light conditions (Fig. 2). An interaction of light with seedling origin was found for leaf area, leaf biomass and shoot biomass (Table 2, Fig. 2), suggesting a significant difference in response to light between two population types. By contrast, interaction of water regime with seedling origin did not significantly affect leaf area or leaf biomass (Table 2, Fig. 2), which suggests that response to water did not differ between them.

Discussion

It is generally believed that exotic plants have greater resource use efficiency relative to native species (Davis et al. 2000; Ehrenfeld 2003; Tilman 1999). In the present study, relative growth of *S. sebiferum* was significantly higher than that of *S. scoparium* when they were competing against each other in identical environments. This suggests that *S. sebiferum* used light and water resources more efficiently than native resident *S. scoparium* grasses. On the other hand, seedling performance was greater for invasive populations than for native populations under favorable conditions in intraspecific experiment, suggesting that higher resource use efficiency of *S. sebiferum* could be evolved in the introduced range rather than pre-adapted in the native range. It has been shown that invasive populations can accelerate soil carbon and nitrogen processes, and use soil nutrients more efficiently than native populations of *S. sebiferum* (Zou et al. 2006). Greater light use efficiency of invasive populations relative to native populations is probably due to increased leaf area rather than the number of leaves (Table 2). In a previous study, we found that TLA and net CO_2 assimilation in terms of leaf area or leaf mass contributed the most to the difference in growth between two population types of *S. sebiferum* (Zou et al. 2007). These newly evolved traits would give rise to *S. sebiferum* outcompeting native *S. scoparium* grasses, particularly when light is limited. ANOVA also showed that the difference in *S. sebiferum* seedling growth was more strongly affected by light than water regime, and the effect of water regime was controlled by light availability (Table 2).

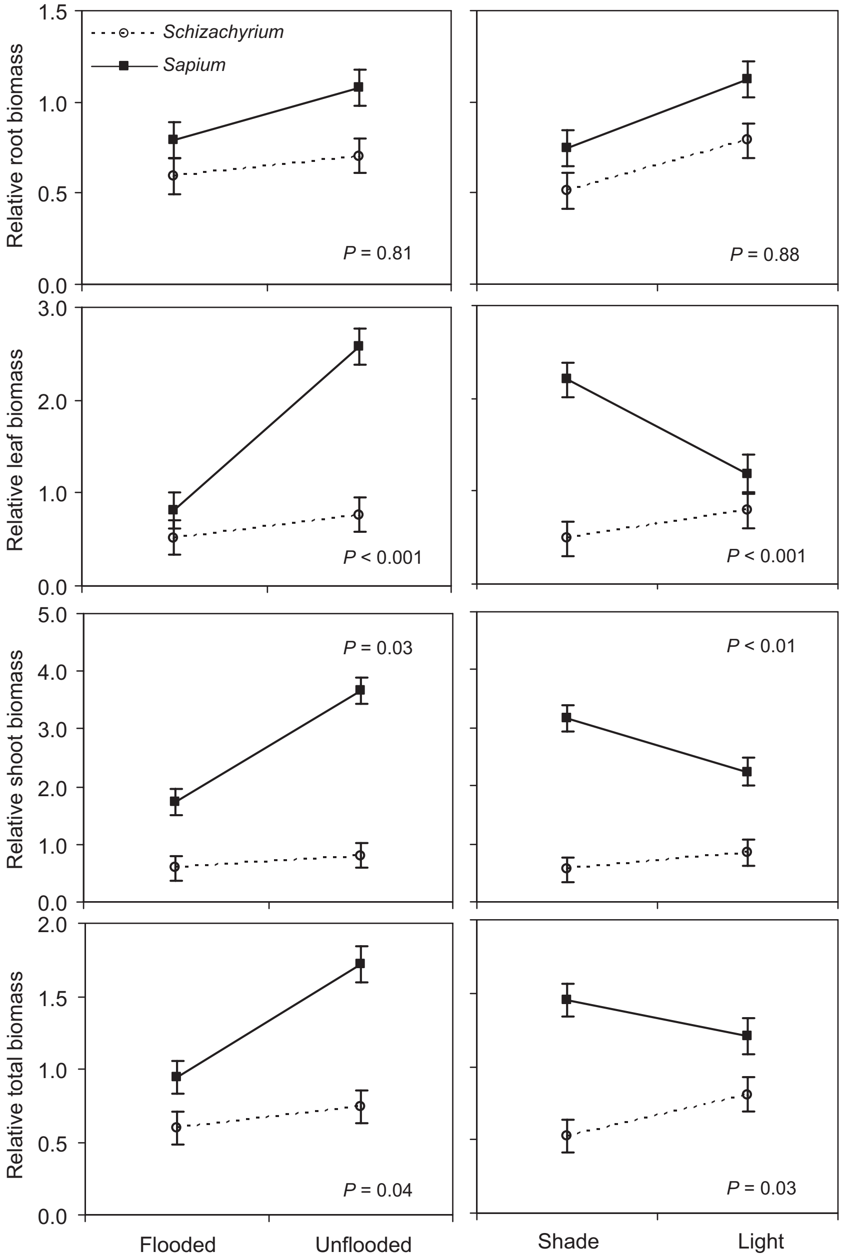

Fig. 1. Growth reaction norms of invasive *Sapium sebiferum* seedlings and native *Schizachyrium scoparium* grasses to water and light conditions. Growth traits of different treatments were normalized to those of flooded–shaded treatments for each species. Error bars represent S.E. The *P*-value reflects the statistical difference in reaction norm between two species, which was represented by the interaction of resource (water regime or light) with species (see Table 1).

This suggests that light availability relative to water regime plays a more important role in the growth of *S. sebiferum* in the introduced range.

Plasticity of invasive plants to different environments may result in higher fitness under unfavorable environments or favorable environments, which reflects two different fitness reaction norm patterns: jack-of-all trades or master-of-some (Richards et al. 2006). The jack-of-all trades pattern confers invasive plants greater ecological breadth, while the master-of-some pattern allows invasive plants to increase population densities under favorable conditions. Consistent with our prediction, plasticity of *S. sebiferum* to light or water was significantly greater than that of *S. scoparium*. However, the reaction norm to light differed from that to water. The reaction norm of *S. sebiferum* to water reflected a master-of-some pattern because *S. sebiferum* was better able to respond with increased growth in favorable soil water conditions (Fig. 1). By contrast, the reaction norm of *S. sebiferum* to light referred to a pattern of

Table 2. ANOVAs for the effects of shading (L, 15% ambient light) and flooding (W) on growth of seedlings from native and invasive populations of *Sapium sebiferum*

Source	d.f.	Height growth			Leaf area			Leaf biomass			Aboveground biomass		
		SS	*F*	*P*	*SS*	*F*	*P*	*SS*	*F*	*P*	*SS*	*F*	*P*
L	1	11340	214.0	<**0.001**	756	3005.6	<**0.001**	11.51	3585.2	<**0.001**	19.87	5417.4	<**0.001**
W	1	1436	17.6	**0.003**	192	1070.2	<**0.001**	2.44	970.3	<**0.001**	3.02	823.0	<**0.001**
O	1	3077	25.5	**0.001**	18	132.1	<**0.001**	0.22	140.7	<**0.001**	0.42	164.1	<**0.001**
P (O)	8	965	2.4	0.42	1	1.1	0.69	0.01	1.5	0.77	0.02	1.6	0.71
L × W	1	2445	29.0	**0.001**	128	408.2	<**0.001**	1.39	297.8	<**0.001**	1.52	264.2	<**0.001**
L × O	1	3	0.0	0.83	14	54.7	<**0.001**	0.16	51.2	<**0.001**	0.21	57.0	<**0.001**
L × P (O)	8	424	0.6	0.74	2	0.8	0.62	0.03	0.7	0.69	0.03	0.6	0.73
W × O	1	3	0.0	0.85	1	4.4	0.07	0.01	2.8	0.13	0.02	6.1	**0.04**
W × P (O)	8	654	1.0	0.52	1	0.6	0.78	0.02	0.5	0.80	0.03	0.6	0.73
L × W × O	1	23	0.3	0.62	0	0.8	0.41	0.02	3.4	0.10	0.00	0.0	0.90
L × W × P (O)	8	675	0.8	0.60	3	0.6	0.80	0.03	0.7	0.72	0.05	0.5	0.86
Model	39	21045	5.1	<**0.001**	1116	51.7	<**0.001**	15.84	58.2	<**0.001**	25.18	55.0	<**0.001**
Error	120	12589	66	0.84	1.41								

O, continental origin of populations (native versus invasive); P, population within the continent as a random effect.

jack-of-all trades, because invasive *S. sebiferum* species had more robust growth in the face of stressful light conditions (Fig. 1). This suggests that decreasing light availability increases *S. sebiferum* tree invasion by limiting the growth of resident herbaceous vegetation more than that of trees (Rogers & Siemann 2003; Siemann & Rogers 2003a). The increase in *S. sebiferum* growth in shade likely reflects this strong positive indirect effect.

Greater resource use efficiency and plasticity of exotic plants relative to resident species may contribute to their invasive success in the introduced range (Baker 1965; Rice & Mack 1991; Richards et al. 2006; Sexton, McKay, & Sala 2002; Sultan 2004). As woody plants invade grasslands, mature woody plants may reduce light availability to grasses and forbs and to woody seedlings as well (Scholes & Archer 1997; Wilson 1998). Wilson (1998) suggested that shading by mature trees may favor woody seedlings in competition with grasses by favoring plants with low root:shoot ratios (i.e., woody plants) over plants with high root:shoot ratios (i.e., grasses). Such a positive feedback appears to indeed promote rapid grassland *S. sebiferum* forest transitions (Siemann & Rogers 2003a). It has also been proposed that flooding facilitates invasion of wet coastal grasslands by *S. sebiferum*, because it is unusually tolerant of prolonged flooding and anaerobic soil conditions (e.g., Bruce et al. 1997; Butterfield, Rogers, & Siemann 2004; Conner 1994; Jones & Sharitz 1990). Jones and Sharitz (1990) found that *S. sebiferum* seedlings showed several morphological adaptations to prolonged flooding. This suggests that flooding might give *S. sebiferum* an advantage in competition with *S. scoparium*.

Relative to native species, greater plasticity of invasive plants may reflect their innate characteristics or evolutionary changes in the introduced range. In the present study, we found a significant difference in growth response to light between native and invasive populations of *S. sebiferum*, suggesting that greater plasticity of *S. sebiferum* is evolved in the introduced range. This evolved greater plasticity of *S. sebiferum* resulted in higher tolerance to shade than resident *S. scoparium* grasses. By contrast, no significant difference in response of growth to water existed between the two population types of *S. sebiferum*, suggesting that the greater plasticity of *S. sebiferum* relative to *S. scoparium* reflects innate characteristics that are pre-adapted in the native range. Indeed, *S. sebiferum* trees are distributed across a wide range of soil water conditions, from dry uplands to riversides in China (Zhang & Lin 1994).

Greater phenotypic plasticity as the result of the combination of its innate properties and newly evolved characteristics suggests that the invasion success of exotic plants would be the outcome of both ecological interactions and evolutionary changes. However, very few studies have examined plasticity of invasive plants at the intraspecific level within an invasive species. Kaufman and Smouse (2001) found that growth traits except leaf shape of invasive Floridian populations versus native Australian populations of *Melaleuca quinquenervia* were plastic in response to pH and water, with plants generally being more plastic in response to pH changes. DeWalt et al. (2004) found no difference in phenotypic plasticity of growth traits to light between native and invasive populations of the tropical shrub *Clidemia hirta*. In the context of plant invasions, no studies simultaneously examined plasticity of invasive plants at both interspecific and intraspecific levels, and thus these studies should be emphasized in the future.

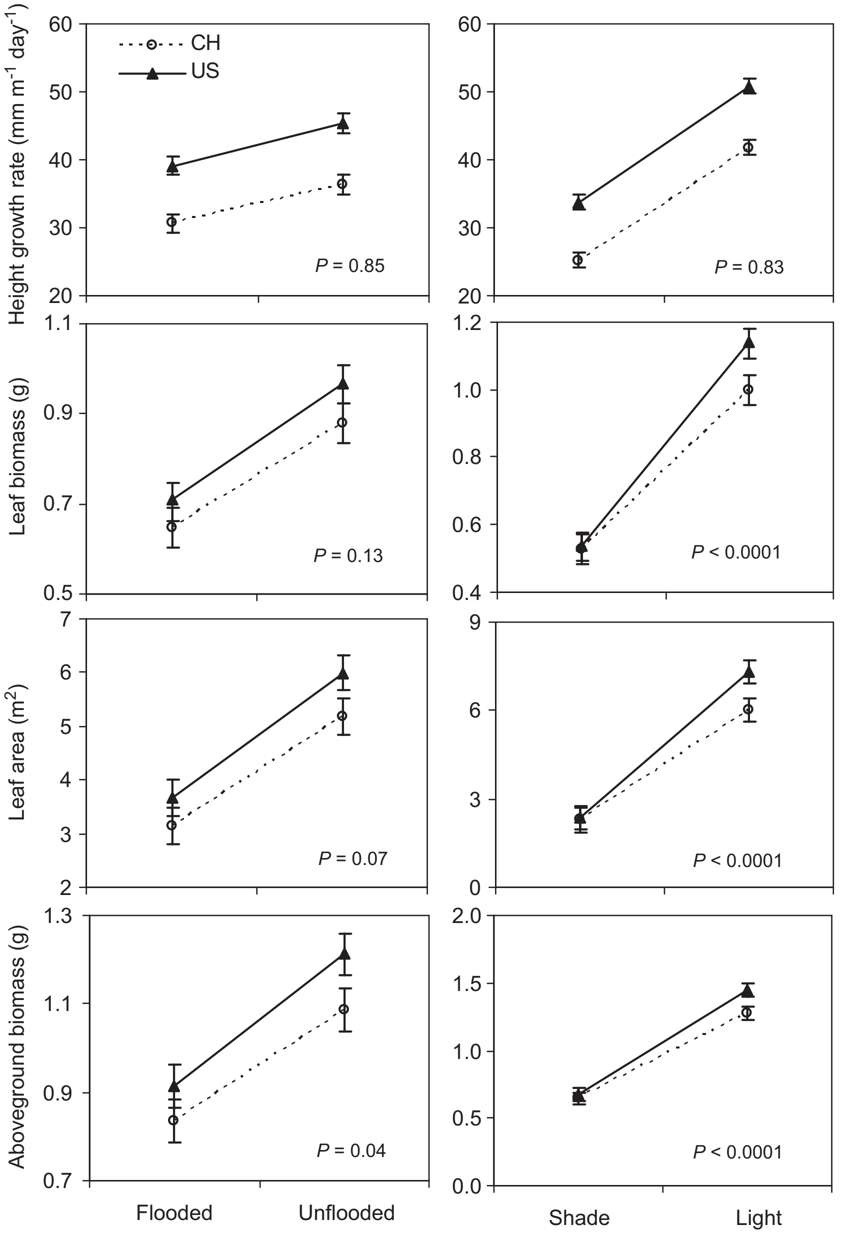

Fig. 2. Growth reaction norms of invasive and native populations of *Sapium sebiferum* to water and light conditions. Error bars represent S.E. The *P*-value reflects the statistical difference in reaction norm between two population types, which was represented by the interaction of resource (water regime or light) with origin (see Table 2).

Limitations of experimental designs

The interspecific experiment attempted to mimic natural field conditions with *S. sebiferum* invading established prairie. Since the average starting biomass of *S. scoparium* was greater than that of *S. sebiferum*, it is possible that an increase in biomass might be more easily achieved by *S. sebiferum* than *S. scoparium.* This could influence the difference in plasticity between the two species. In addition, the emphasis on relevance to prairie invasions in the interspecific experiment versus the focus on individual performance to maximize our ability to detect genetic differences in plasticity in the intraspecific experiment places limits on the inferences that can be drawn from this study. Finally, there might also have been interactions with soil type, since the two experiments used different local soils that likely differed in their physical properties as well as their biotic components. However, other experiments in the introduced range with *S. sebiferum* from US populations grown individually in pots show the same qualitative patterns with shading (i.e., reduced growth in shade;

Rogers & Siemann 2002) and flooding (i.e., reduced growth in flooded conditions; Butterfield et al. 2004) as we found for plants grown individually in pots in China (Fig. 2).

Conclusions

Different plasticity mechanisms may have different implications for plant invasion success. Relative to *S. scoparium*, the greater plasticity to water conditions would benefit *S. sebiferum* establishing in the introduced range with a wide breadth of soil water status at a lower cost. In response to light conditions in the introduced range, selection could favor *S. sebiferum* evolving tolerance to shade, which may help to explain why *S. sebiferum* became invasive long after it was introduced. Relatively, greater plasticity of *S. sebiferum* to variation in water conditions may play a key role in its early establishment, while that to light conditions may play a more important role in later phases of invasion.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2007.11.010.

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