

The role of soil resources in an exotic tree invasion in Texas coastal prairie

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Summary

1 Variation in resource requirements among plant species may cause changes in community composition when resource supply rates vary. Because exotic plants may differ in their requirements compared with native plants, changes in resource levels or ratios may change their invasive potential. The concentration hypothesis, nutrient balance hypothesis and resource ratio hypothesis make different predictions regarding the effects of nutrient additions on plant communities and the success of invaders.

2 We investigated these hypotheses using Chinese tallow tree (*Sapium sebiferum*), which is an aggressive invader of grasslands in the southern USA. Soil nitrogen, phosphorus and potassium were manipulated in a full factorial field experiment in a Texas coastal prairie.

3 Survival of *Sapium* seedlings over three growing seasons was independent of all three types of nutrient additions, alone or in any combination. Adding nitrogen or potassium increased the mass and height of *Sapium* seedlings. Adding phosphorus increased the mass and height of *Sapium* seedlings only when nitrogen was also added. These results support the nutrient balance hypothesis, which assumes that higher tissue concentrations of a nutrient reflect a greater ability of a plant species to take up and/or conserve that nutrient.

4 The above-ground biomass of background prairie vegetation was independent of the addition of each type of nutrient alone or in any combination. However, the functional composition of the community shifted from graminoids to forbs with the addition of nitrogen and from graminoids to woody plants with the addition of phosphorus. These results support the concentration hypothesis, which assumes that higher tissue concentrations of a nutrient reflect a greater requirement for that nutrient. The contrasting responses of native woody vegetation and *Sapium* to phosphorus addition suggest that *Sapium* may have unusually low demands for phosphorus relative to nitrogen for a woody plant in this community.

5 These results show that potassium or nitrogen addition, perhaps in combination with phosphorus addition, has the potential to accelerate the invasion of *Sapium* into Texas coastal prairies. Because anthropogenic nutrient additions are common in grasslands worldwide, this may help to explain the frequent success of woody species invading grasslands.

Key-words: Chinese tallow tree, light, nitrogen, phosphorus, potassium, *Sapium sebiferum*

Journal of Ecology (2007) **95**, 689–697

doi: 10.1111/j.1365-2745.2007.01253.x

Introduction

Plants vary in their nutrient requirements both within and among habitats, and variations in resource requirements among plant species may allow changes in the

supply rates of resources to modify community composition (Gusewell & Bollens 2003; Stevens *et al.* 2004; Crawley *et al.* 2005). Exotic plants may differ in their requirements compared with native plants and, as such, changes in soil resource levels or ratios have the capacity to change their invasive potential (Harpole 2006). In addition, differences in herbivory or diseases between exotic and native plants (Keane & Crawley 2002) may amplify any pre-existing differences in nutrient requirements. However, even for communities of native plants there is debate on how differences in nutrient

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requirements are related to differences in plant nutrient content, and making *a priori* predictions is difficult for field experiments. As a result, proper tests of prevailing theories are few in terrestrial ecosystems (Miller *et al.* 2005).

Resource competition theory typically infers higher nutrient requirements for species of plants that have higher tissue concentrations of that nutrient compared with plants with lower tissue concentrations (Tilman 1982; hereafter 'concentration hypothesis'). Perhaps the most successful applications of this body of theory use the nutrient requirements necessary to achieve non-zero population equilibria in single species cultures to predict the outcome of competition between two species (Miller *et al.* 2005). The link from plant traits (e.g. root : shoot ratios) to competitive ability for soil resources vs. light has proven to be a successful predictor of competition as well (Wilson 1998). Although it is comparatively more difficult to generate predictions of competition for soil resources from nutrient concentrations within plants, there have been some examples of successful applications in which plant species with lower tissue concentrations also are better competitors for that nutrient (Tilman & Wedin 1991). However, two assumptions help to do this in general (Tilman 1982). First, optimal foraging theory predicts that plants will consume nutrients in proportion to their limitation by those nutrients. Second, trade-offs between nutrient-dependent maximal growth rates and efficiency of nutrient use predict that plants with high nutrient concentrations should have high maximal growth rates (Grime 1977). Together these allow predictions of effects of nutrient supply on the outcome of competition to be generated from analyses of plant nutrient content. Specifically, it is predicted that increasing the supply of a nutrient will favour plants with high tissue concentrations (and presumably high nutrient requirements), in competition with plants with low tissue concentrations, and presumably low requirements.

In contrast, in agricultural systems it is typically assumed that lower tissue concentrations of a nutrient indicate a larger deficit of that nutrient compared with a plant's requirements for that nutrient (hereafter 'nutrient balance hypothesis'). In fact, analyses of concentrations of nutrients in plant tissues are routinely used to prescribe fertilizer amendments in agricultural systems. However, the recommendations for fertilizer inputs vary with each crop based on experimental measurements of growth rates vs. tissue nutrient concentrations and soil nutrient concentrations (Kalra 1997). In the absence of such species-specific information, it is parsimonious to assume that plants have comparable requirements and that, in general, a lower concentration of a nutrient in a plant's tissue indicates a larger unmet need for that nutrient. In such a case, it is predicted that increasing the supply of a nutrient will give a larger benefit to plants with low tissue concentrations, and presumably high unmet requirements, in competition with plants with high tissue concentrations and presumably low unmet requirements.

Another body of theory extends simple resource competition models and posits that the differences in the relative requirements of resources are more informative for predicting the effects of changes in nutrient supply than are the absolute supply rates of nutrients considered separately (Tilman 1988; Grover 1997). Indeed, this approach to understanding the relative nutrient limitation of different species, functional groups or trophic levels is the foundation of the field of ecological stoichiometry (Sterner & Elser 2002). In a manner similar to the concentration hypothesis, higher relative concentrations of a nutrient in plant tissues compared with another nutrient are assumed to be indicative of a higher relative need for that nutrient. Furthermore, such ratios are also assumed to be predictive of the relative limitation of different species by different nutrients (Harpole 2006). It is predicted that changes in the relative supply rates of a pair of resources will favour the plant species that has tissue concentrations more similar to this new ratio of nutrient supply (hereafter 'resource ratio hypothesis').

There are examples of changes in nutrient supply rates impacting the abundance of exotic plants. For instance, it has been shown that the intensity of weed infestation may depend on the amount of nitrogen fertilization relative to other limiting nutrients (Jornsgard *et al.* 1996; Busey 2003). The availability of nitrogen relative to potassium may influence barberry invasions in the north-east United States and the success of dandelions (Tilman *et al.* 1999; Cassidy *et al.* 2004). Invasion of birch into bogs is stimulated by nitrogen additions (Tomassen *et al.* 2003, 2004), whereas phosphorus additions have been shown to decrease exotic grass invasion into pine savannas (Brewer & Cralle 2003). Other studies have been unable to show any effect of soil resource ratios on invasions (e.g. LeJeune *et al.* 2006). In general, comparisons of co-occurring native and exotic plants indicate that resource conditions are often important in determining their relative performances (Daehler 2003). However, many of the studies have been carried out in the glasshouse, limiting the insights that can be gained from them. Furthermore, in most of these studies, a single nutrient was added, which makes it difficult to separate the effects of the addition of the nutrient *per se* from effects mediated through increased productivity. Indeed, the relative importance of competition for soil resources vs. light may be affected by the addition of a single soil element (Li & Wilson 1998; Wilson 1998). Factorial nutrient addition field experiments are necessary to isolate these different mechanisms, particularly in cases where exotic plants differ in growth form (e.g. graminoid vs. woody) or nutrient use efficiency from the background vegetation.

FOCAL SPECIES

The exotic Chinese tallow tree [*Sapium sebiferum* (L.) Roxb., Euphorbiaceae, hereafter '*Sapium*'; nomenclature follows Hatch *et al.* (1990); synonym *Triadica sebifera*

(L.) Small] is invasive in the southern United States (Bruce *et al.* 1997; Siemann *et al.* 2006). It grows rapidly, has oil-rich seeds and colourful autumn foliage, and has been widely planted as a potential biomass or oil crop and as an ornamental. *Sapium* is naturalized from the Gulf Coast of Texas to the Atlantic Coast of North Carolina. It aggressively displaces native plants and forms monospecific stands within decades of its appearance in a prairie. In the Gulf Coast much coastal prairie has been converted to *Sapium* woodland thickets (Bruce *et al.* 1997). Fire can reduce *Sapium* invasion in the early stages of invasion (Grace 1998; Hartley *et al.* 2007) but this may be less likely in the most productive conditions (our unpublished data).

Sapium invasion into prairies is accelerated by decreases in light availability and increases in nitrogen availability, such as found in the vicinity of early pioneer trees (Siemann & Rogers 2003b). Because *Sapium* has greater relative allocation above ground compared with grasses (i.e. low root : shoot), decreases in light and increases in soil resources that increase the relative availability of soil resources vs. light are expected to increase *Sapium*'s competitive success in a grass-dominated ecosystem (Li & Wilson 1998; Wilson 1998). However, it is not known whether the increased success of woody plants, such as *Sapium*, in grasslands that occurs with nitrogen addition also occurs with the addition of other soil resources or is a specific effect of nitrogen addition. If woody plants are particularly responsive to changes in one or more soil resource, do the same nutrients increase *Sapium*'s success or does it have an unusual response due to its exotic status?

The three theories differ in that the concentration and resource ratio hypotheses focus on resource-dependent population equilibria whereas the nutrient balance hypothesis focuses on individual physiological requirements. But, population and physiological responses need not be positively correlated across treatments. For *Daphnia* species, however, the ranking of species for physiological and population resource requirements were shown to be the same (Kreutzer & Lampert 1999), which suggests that individual- and population-based

theories may both be useful in predicting invasion intensity and dynamics in the case of *Sapium* as well.

STUDY SITE

The University of Houston Coastal Center is a 374-ha research area located ~50 km south-east of Houston, TX, USA (for a site description, see Siemann & Rogers 2003a). Historically, this site was mostly tallgrass prairie. Some areas have been invaded by *Sapium* while others have been protected from invasion by annual mowing. Mowed areas are dominated by graminoids (~60% of cover at the start of this experiment in this field), with *Schizachyrium scoparium* (Michx.) Nash, *Andropogon glomeratus* (Walt.) B.S.P. and *Muhlenbergia capillaris* (Lam.) Trin. as the main species in the field in which this experiment took place (our unpublished data). Forbs [~10% of cover, main species in this field: *Euthamia leptocephala* (T. & G.) Greene, *Helianthus angustifolius* L., and *Gaura longiflora* Spach] and woody plants [~30% of cover, main species in this field: *Rubus riograndis* Bailey, *Myrica cerifera* L. and *Berchemia scandens* (Hill) K. Koch] are also abundant. Mowing was stopped in the experimental plots for the duration of these studies. Average annual rainfall is 1070 mm distributed fairly evenly throughout the year. Average temperature is 20.9 °C. Soils are expansive Lake Charles Clay Vertisols (fine, montmorillonitic, thermic Typic Pelludert) with a 40–60% clay content.

NUTRIENT CONTENT OF VEGETATION

Previously published analyses of the carbon, nitrogen and phosphorus content of functional groups of plants at UHCC and of *Sapium* (Lankau *et al.* 2004) showed that *Sapium* has unusually low concentrations of nitrogen compared with native woody plants at that site (Table 1). Only graminoids had lower concentrations of nitrogen in their above-ground mass than *Sapium*. By contrast, *Sapium* had higher concentrations of phosphorus than any other groups of plants at UHCC (Table 1). There are no published data on potassium

Table 1 Carbon, nitrogen and phosphorus content of vegetation at UHCC as percentage dry mass (mean $\pm$ SE, from Lankau *et al.* 2004). N : P is the mass ratio of nitrogen to phosphorus. Predicted changes in relative abundances of functional groups and invasion success of *Sapium* with nitrogen and phosphorus addition are shown for the concentration hypothesis (CH), nutrient balance hypothesis (NBH), and resource ratio hypothesis (RRH). N– or P– and N+ or P+ indicate predicted decreases and increases in relative abundances with nitrogen or phosphorus addition. N $\times$ P ($\pm$) indicates that the effects of nitrogen and phosphorus addition are opposite and offset each other in combination. Significant effects are shown in the results column. P+ if N indicates that phosphorus has a positive effect if added together with nitrogen

Type of vegetation	%C	%N	%P	N:P	CH	NBH	RRH	Results
Graminoids	42.8 $\pm$ 0.4	0.84 $\pm$ 0.06	0.060 $\pm$ 0.004	12.7 : 1	N– P–	N+ P+	N $\times$ P ($\pm$)	P–
Forbs	39.8 $\pm$ 0.9	1.51 $\pm$ 0.01	0.081 $\pm$ 0.004	18.9 : 1	N+ P–	N– P+	N $\times$ P ($\pm$)	
Woody	44.8 $\pm$ 0.4	1.98 $\pm$ 0.40	0.135 $\pm$ 0.055	14.1 : 1	N+ P+	N– P–	N $\times$ P ($\pm$)	P+
<i>Sapium</i> seedling	44.8 $\pm$ 0.3	0.98 $\pm$ 0.35	0.160 $\pm$ 0.015	6.1 : 1	N– P+	N+ P–	N $\times$ P ($\pm$)	N+ N $\times$ P (P+ if N)
Graminoids : forbs					N– P–	N+ P+	N $\times$ P ($\pm$)	N–
Graminoids : woody					N– P–	N+ P+	N $\times$ P ($\pm$)	P–
Forbs : woody					N– P–	N+ P+	N $\times$ P ($\pm$)	

concentrations at this site or any other coastal tallgrass prairies but we included potassium additions in our experimental design because it is the other major soil nutrient that is commonly limiting.

PREDICTIONS

We conducted a grassland field experiment with *Sapium* seedlings to test the following predictions. (i) If a higher concentration of a nutrient in a plant indicates a lower use efficiency but higher resource-dependent maximal growth rate for that nutrient (concentration hypothesis), then addition of a nutrient will increase the relative abundance of species with higher concentrations of that nutrient. Nitrogen fertilization will favour native forbs and woody plants in competition with native grasses and *Sapium* seedlings. Phosphorus fertilization will favour *Sapium* seedlings and native woody plants in competition with native forbs and grasses. (ii) If a lower concentration of a nutrient in a plant reflects greater limitation of growth by that nutrient (nutrient balance hypothesis), then addition of a nutrient will increase the relative abundance of species with lower concentrations of that nutrient. Nitrogen fertilization will favour native grasses and *Sapium* seedlings in competition with native forbs and woody plants. Phosphorus fertilization will favour native forbs and grasses in competition with *Sapium* seedlings and native woody plants. (iii) If a higher N : P ratio indicates greater limitation by phosphorus relative to nitrogen (resource ratio hypothesis), then nitrogen fertilization will favour, but phosphorus fertilization will be detrimental to, *Sapium* seedlings and native woody plants in competition with native forbs and grasses.

Methods

EXPERIMENT DETAILS

We used a completely randomized factorial design with 64 plots (2 × 2 m with 2-m semi-annually mowed buffer zones between adjacent plots) that received three treatments: N (fertilization or no), P (fertilization or no) or K (fertilization or no). Nitrogen fertilization plots received 8 g m⁻² yr⁻¹ of N applied as ammonium nitrate in May and June (i.e. 4 g m⁻² each time). Phosphorus fertilization plots received 3.5 g m⁻² yr⁻¹ of P applied as triple superphosphate in May and June. Potassium fertilization plots received 6.7 g m⁻² yr⁻¹ of K applied as muriate of potash (ClK₂O). Fertilizers were applied by broadcasting dry fertilizer over plots by hand. With these amounts, the NPK plots received a mix of fertilizer equivalent to equal parts nitrogen, phosphate and potash (i.e. on a fertilizer label the three numbers would be equal). Following spreading of fertilizer(s), every plot (including those which did not receive N, P or K) was watered with approximately 8 L of water to help soak the fertilizer into the soil. The entire experiment was fenced with a low (60 cm high) barbed wire fence to

exclude feral pigs. The experiment ran for three growing seasons (876 days).

In November and December 2000, we collected seed from *Sapium* trees at the University of Houston Coastal Center. In January, seeds were planted into flats in an unheated glasshouse with open vent flaps. Seeds began to germinate in March, which is approximately the time the first seedlings appeared in the field. After a seed germinated, it was transferred to a 100-mL Conetainer (Stuewe & Sons, OR, USA) filled with 1 cm of peat moss and 12 cm of commercially available topsoil. Seedlings were grown in the glasshouse until they had two sets of true leaves, then grown outside under a 50% shade cloth to 'harden off'. Seedlings were transplanted into the field (one per plot) in April 2001.

DATA COLLECTION

Sapium seedling survival was checked three times during each growing season (early May, early July and early October). When seedlings were checked in July and October, we also recorded seedling height (from ground to the terminal bud), counted the number of leaves, and estimated the average percentage of leaves removed by chewing herbivores. In September 2003, seedlings were clipped at ground level, then dried and weighed.

Vegetation cover by functional group (graminoid, forb or woody) was estimated twice during each growing season. At the end of the second and third growing seasons, we measured light penetration to ground level. We used an 80-cm-long, 80-sensor ACCUPAR linear photosynthetically active radiation (PAR) ceptometer (Decagon, Pullman, WA, USA) with an external point sensor (LICOR, Lincoln, NE, USA) to measure light availability above and below the vegetation in a single location in each plot. We took PAR measurements twice during each growing season (June and August) at midday on cloud-free days. At the end of the first growing season, we clipped the vegetation at ground level in a 0.2-m² area (20 cm × 1 m) of each plot away from the transplanted seedling, then dried and weighed the clipped vegetation. At the end of the third growing season (September 2003), we repeated this clipping in a different area of the plot than in the first year.

Results

SEEDLING PERFORMANCE

Survival of *Sapium* seedlings was independent of all experimental treatments. First, we fitted survival time data with an exponential model in a parametric survival analysis (Siemann & Rogers 2006; Statview 5.0, SAS Inc.) to examine the dependence of *Sapium* seedling survival time on our treatments. We handled our experimental treatments as categorical covariates and used likelihood-ratio tests to determine that survival time did not depend on our experimental treatments alone or

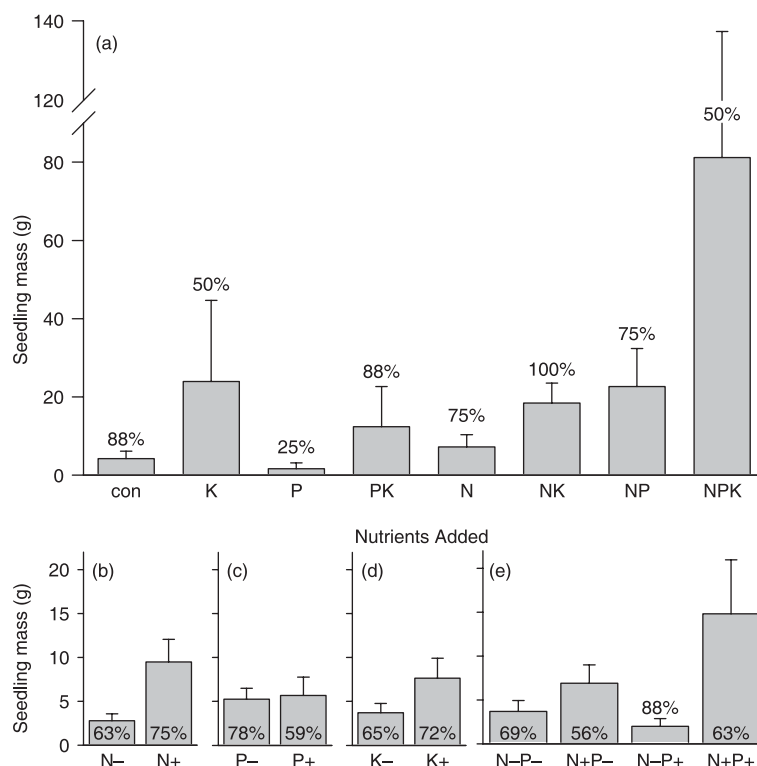


Fig. 1 Dependence of mass of surviving seedlings (+ SE) on (a) full three-way nutrient addition treatment, (b) nitrogen addition treatment, (c) phosphorus addition treatment, (d) potassium addition treatment, and (e) combination of nitrogen and phosphorus addition treatments. Percentages indicate the survival of seedlings in that treatment.

Table 2 The dependence of *Sapium* seedling survival (exponential model), *Sapium* seedling height (ANOVA), and *Sapium* seedling mass (log-transformed, ANOVA) on experimental additions of nitrogen, phosphorus and potassium

Factor	Seedling survival			Seedling mass			Seedling height	
	d.f.	χ^2	<i>P</i>	d.f.	F_{36}	<i>P</i>	F_{36}	<i>P</i>
N	1	0.1	0.76	1	7.7	< 0.01	8.2	< 0.01
P	1	0.5	0.46	1	0.4	0.51	< 0.1	0.83
K	1	< 0.1	0.94	1	5.9	< 0.05	4.7	< 0.05
N × P	2	4.3	0.72	1	4.5	< 0.05	4.3	< 0.05
N × K	2	0.7	0.96	1	0.1	0.83	< 0.1	0.86
P × K	2	0.6	0.76	1	0.3	0.60	< 0.1	0.98
N × P × K	3	0.7	0.88	1	0.3	0.62	0.1	0.80
Model				7	2.7	< 0.05	2.5	< 0.05
Model r^2						0.35		0.33

in any combination [Fig. 1 (final survival percentages above bars), Table 2]. Second, we performed a survival analysis using the Kaplan–Meier model in a non-parametric survival analysis (Siemann & Rogers 2006; Statview 5.0, SAS Inc.). We used Mantel–Cox tests to examine whether survival time depended on our experimental treatments (Siemann & Rogers 2006; main effects only). No factors had an effect on *Sapium* seedling survival in the non-parametric analyses (nitrogen $P = 0.32$, phosphorus $P = 0.09$, potassium $P = 0.72$). Forty-four of the 64 seedlings survived to the final harvest.

We used ANOVA to examine the effect of treatments on *Sapium* seedling growth (Statview 5.0, SAS Inc. for all ANOVAs). Throughout, we report unmodified P -values from individual analyses. Above-ground *Sapium* seed-

ling mass was log-transformed to meet assumptions of ANOVA and back-transformed for graphical presentation with standard errors approximated by adding the transformed standard errors to the transformed means before back transforming [i.e. $\exp(\text{mean} + \text{SE})$]. Both *Sapium* mass (Fig. 1) and height (Fig. 2) at the end of the third growing season were higher in plots that received nitrogen or potassium (Table 2). Phosphorus only increased seedling mass or height in combination with nitrogen addition (i.e. significant $N \times P$ term, Table 2).

COMMUNITY RESPONSES

We used ANOVA to examine the effect of treatments on peak standing crop of the background vegetation. Vegetation

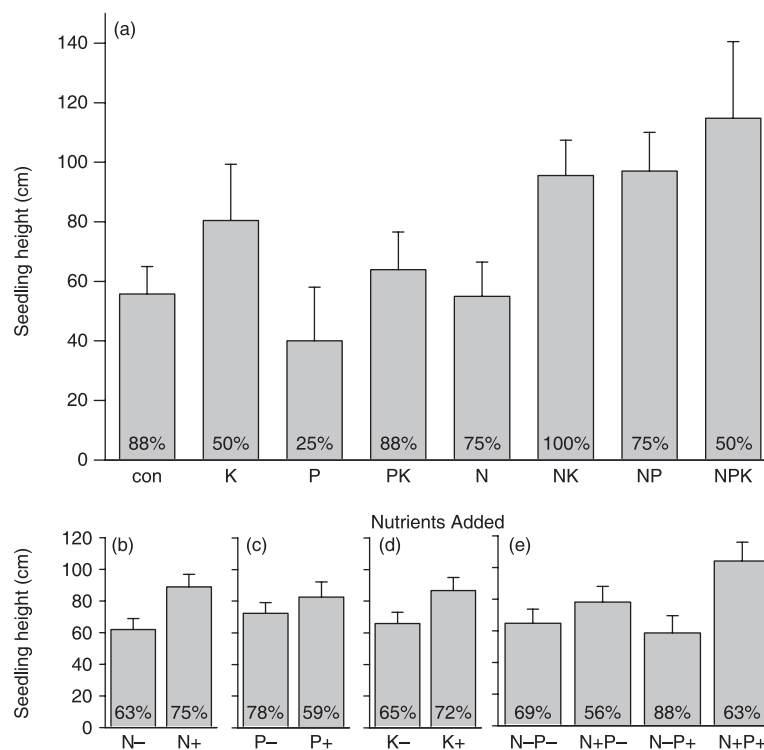


Fig. 2 Dependence of height of surviving seedlings (+ SE) on (a) full three-way nutrient addition treatment, (b) nitrogen addition treatment, (c) phosphorus addition treatment, (d) potassium addition treatment, and (e) combination of nitrogen and phosphorus addition treatments. Percentages indicate the survival of seedlings in that treatment

Table 3 The dependence of vegetation mass, percentage cover within functional groups, and the relative cover within pairs of functional groups on experimental additions of nitrogen, phosphorus and potassium in ANOVAS.

Factor	d.f.	Vegetation mass		Graminoids		Forbs		Woody		Graminoids : forbs		Graminoids : woody		Forbs : woody	
		F_{56}	P	F_{56}	P	F_{56}	P	F_{56}	P	F_{56}	P	F_{56}	P	F_{56}	P
N	1	1.4	0.26	0.1	0.78	< 0.1	0.99	< 0.1	0.80	4.3	< 0.05	0.2	0.64	1.5	0.22
P	1	0.4	0.45	5.4	< 0.05	0.3	0.56	5.0	< 0.05	1.6	0.21	4.3	< 0.05	1.8	0.18
K	1	0.2	0.71	0.2	0.64	0.3	0.56	0.3	0.60	0.6	0.43	0.1	0.73	0.4	0.51
N × P	1	0.6	0.55	0.1	0.79	2.1	0.15	0.3	0.63	1.5	0.23	0.3	0.58	1.8	0.18
N × K	1	0.1	0.60	1.1	0.29	2.1	0.15	0.5	0.46	< 0.1	0.96	1.4	0.24	0.5	0.49
P × K	1	3.0	0.07	1.0	0.31	0.8	0.38	1.2	0.28	< 0.1	0.76	< 0.1	0.92	0.2	0.68
N × P × K	1	0.7	0.35	< 0.1	0.84	0.3	0.56	< 0.1	0.78	< 0.1	0.94	0.4	0.51	0.5	0.47
Model	7	1.0	0.43	1.1	0.34	0.9	0.54	1.1	0.41	1.2	0.33	1.0	0.46	1.0	0.47
Model r^2			0.11		0.13		0.10		0.11		0.13		0.11		0.11

mass was log-transformed to meet the assumptions of ANOVA and back-transformed for graphical presentation. No treatment alone or in combination affected vegetation mass (Table 3, Fig. 3). No predictor affected vegetation mass in models of reduced dimension (i.e. no three-way interaction term or no interaction terms). Adding covariates for percentage of vegetation that was graminoid or woody vegetation in a pair of ANOVAS did not change the lack of any significant predictors of vegetation mass. In a one-way ANOVA with an eight-level predictor for the nutrient combination added, nutrient addition combination was not a significant predictor of vegetation mass ($F_{7,56} = 1.0$, $P = 0.45$) and no contrasts were significant (all $P > 0.15$). Light

penetration to ground level was extremely low in both growing seasons (second, 0.9%; third, 1.3%) and independent of all treatments alone or in combination in each year (second year: $F_{7,56} = 0.8$, $P = 0.59$; third year: $F_{7,56} = 1.7$, $P = 0.11$; no F -tests significant for terms in either year).

We used ANOVA to examine the effects of treatments on the functional composition of the vegetation in the plots. Analyses using percentage forb cover (arcsine-transformed), percentage graminoid cover (arcsine-transformed) and percentage woody cover (arcsine-transformed) indicated that phosphorus addition decreased graminoids and increased woody plants but the overall models were not significant (Table 3).

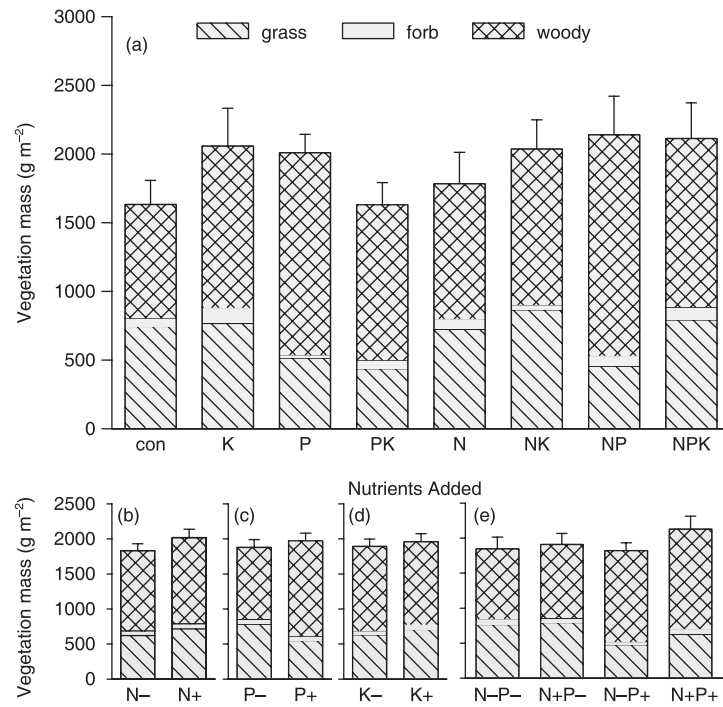


Fig. 3 Dependence of background vegetation mass (+ SE) on (a) full three-way nutrient addition treatment, (b) nitrogen addition treatment, (c) phosphorus addition treatment, (d) potassium addition treatment, and (e) combination of nitrogen and phosphorus addition treatments. The proportions of functional groups within treatment combinations are estimated from percentage cover data.

One-way ANOVAS with individual nutrient factors and these functional groups had the same significant results for phosphorus (graminoid: $F_{1,62} = 5.7$, $P < 0.05$; woody: $F_{1,62} = 5.3$, $P < 0.05$) but no other factors were significant in any analyses. Analyses using the ratios of functional groups indicated that the ratio of graminoid cover to woody cover decreased with phosphorus addition as expected, with a decrease in graminoids and increase in woody vegetation upon phosphorus addition (Table 3). Nitrogen addition decreased the ratio of graminoids to forbs (Table 3). Overall model F -tests were not significant so we performed a set of one-way ANOVAS, which showed a significant effect of phosphorus on the ratio of graminoids to woody plants ($F_{1,62} = 4.6$, $P < 0.05$) and of nitrogen on graminoids to forbs ($F_{1,62} = 4.4$, $P < 0.05$).

Discussion

The positive effects of nitrogen addition on *Sapium* growth indicate that anthropogenic nitrogen addition has the potential to increase the invasion intensity of Chinese tallow trees into coastal tallgrass prairies (Table 2, Figs 2 & 3). The addition of nitrogen had relatively less of an effect on the relative abundance of native woody plants, indicating that the potential growth of *Sapium* is comparatively more limited by nitrogen availability such that it is able to respond more strongly to increases in nitrogen availability. In another experiment with nitrogen as the only soil resource manipulated, seedlings of the native tree hackberry (*Celtis laevigata*), which have nitrogen concentrations that are lower than those in similarly aged *Sapium* seedlings

(Lankau *et al.* 2004), responded positively to nitrogen addition but at a far lower magnitude than *Sapium* seedlings (Siemann & Rogers 2003b). The large increases in *Sapium* growth with nitrogen addition, together with a low concentration of nitrogen in *Sapium* compared with the background vegetation, are consistent with the predictions of the nutrient balance hypothesis.

Sapium appears to have simultaneously high nitrogen use efficiency (as indicated by the low concentration of tissue nitrogen) and a high maximal nitrogen-dependent growth rate (as indicated by the fast growth of seedlings in high nitrogen conditions). Such a combination of traits might suggest that *Sapium* has avoided the trade-off between these characteristics that is assumed in the concentration and resource ratio hypotheses. One mechanism that is thought to underlie this trade-off is ribulose-1,5-bisphosphate carboxylase (rubisco) concentrations. These represent the dominant pool of nitrogen in plants and play a pivotal role in determining photosynthetic rates (Onoda *et al.* 2004). However, differences in leaf structure also seem to play a role in differences in nitrogen use efficiency among plants from different functional groups (Hikosaka *et al.* 1998). It is possible that low losses to herbivores could allow *Sapium* to deviate from the trade-off curve for native plants by having low losses of nitrogen (Burt-Smith *et al.* 2003).

Another possibility is that nitrogen is relatively abundant in these grasslands, in contrast to other tallgrass prairies in North America (Tilman 1987; Dyer *et al.* 1991), such that ambient tissue concentrations of nitrogen do not reflect nitrogen use efficiency. The range of soil nitrogen concentrations at Cedar Creek,

Minnesota, is 357–870 mg kg⁻¹ dry weight (dw) (Inouye *et al.* 1987) whereas it averages 2500 mg kg⁻¹ dw at UHCC (our unpublished data) and Konza, Kansas (Blair 2004). Nitrogen content in little bluestem at Cedar Creek ranges from 0.68% to 1.11% along a gradient of nitrogen fertilization which brackets the concentration found in graminoids here (Table 1). Yet nitrogen fertilization increases plant standing crops at both Cedar Creek and Konza (Tilman 1987; Dyer *et al.* 1991), but not here (Table 3, Fig. 3). Unfortunately, this may mean that comparisons of tissue concentrations in invasive plants and native plants in ambient field conditions even in combination with simple soil chemistry tests may be of little use in predicting the effects of nutrient additions on their invasion success. Rather, experiments such as this one that directly test the effects of different types of fertilization on the success of individual invaders in particular ecosystems may be more informative.

Our results demonstrate that compared with native woody plants, *Sapium*'s growth is more strongly limited by nitrogen availability but less limited by phosphorus availability. Indeed, there was a significant increase in the relative abundance of native woody plants with phosphorus addition (Table 3, Fig. 3) but no effect of phosphorus addition on *Sapium* growth (Table 2, Figs 1 & 2). *Sapium* has been shown to have a greater increase in growth with mycorrhizal associations than any native woody plants (Nijjer *et al.* 2004), which may explain the lesser phosphorus limitation of *Sapium* compared with native woody plants found here. Only after nitrogen was added did phosphorus become limiting to *Sapium* (Table 2, Figs 1 & 2). If nitrogen is being added to a prairie, phosphorus input may increase invasion intensity.

As we did not have data on the potassium content of either *Sapium* or the native vegetation, we did not predict the increase in *Sapium* growth that accompanied potassium addition (Table 2, Figs 1 & 2). Potassium has been shown to increase the invasion success of dandelion (*Taraxacum officinale*) in grasslands (Tilman *et al.* 1999). However, because anthropogenic potassium addition is not as common as nitrogen addition and *Sapium* invasions typically occur in areas that are not deliberately fertilized, this is an interesting result to address in further studies but is unlikely to be of practical use in controlling *Sapium* invasions.

In generating our conclusions about *Sapium* invasion intensity from seedling growth and survival, we assume that other life stages of *Sapium* have similar or stronger responses to soil resource amendments. *Sapium* seed germination depends primarily on the amount of disturbance because *Sapium* is extremely sensitive to temperature fluctuations as a germination cue (Donahue *et al.* 2004, 2006; Nijjer *et al.* 2002). If high soil nutrient availability is positively correlated with disturbance, or independent of disturbance, then our results for seedlings should apply to invasion from seed as well, because our results would be strengthened or unaffected, respectively. Furthermore, time to seed production and amount of seed produced should be positively correlated with

seedling and sapling growth rates. Therefore, the results observed here for seedling responses should indeed be predictive of invasion intensity.

The effect of fertilization on *Sapium* invasion success was better predicted by the nutrient balance hypothesis than by the concentration or resource ratio hypotheses (Table 1). In other work on grassland fertilization and the outcome of competition (e.g. Tilman & Wedin 1991), transient increases in the abundances of species following fertilization may not be indicative of the equilibrium composition of the community. In other words, initially species with high growth rates increase in abundance with nitrogen addition but eventually species that can survive on lower concentrations of nitrogen outcompete them in the long term. In such a situation, the nutrient balance hypothesis would be likely to predict the transient dynamics but not the eventual outcome of competition. In the case of *Sapium* in these grasslands, once *Sapium* is able to grow tall enough to shade the native herbaceous vegetation, the natives no longer occur in the vicinity of the *Sapium* tree (Siemann & Rogers 2003b). As a result, if fertilization causes a transient increase in *Sapium* growth the eventual outcome of competition will not be determined by nitrogen competition but rather by competition for light (Siemann & Rogers 2003b). The change in relative importance of soil resource vs. light competition occurs on a short time scale, not a generation time scale. Thus, the transient dynamics are more closely linked to the outcome of competition than in the case of competition among herbaceous plants (Davis *et al.* 2000). Because anthropogenic nitrogen addition is common in grasslands worldwide (Suding *et al.* 2005), the increase in *Sapium* success we observed here with nitrogen addition may help to explain the frequent success of woody species invading grasslands.

Acknowledgements

We thank G. Aumann, T. Becker, B. Butterfield, J. Hammer, J. Ferris, V. Keener, R. Lankau, Z. McLemore, D. Mee, R. Tardif, E. Urban and T. White for assistance; the University of Houston Coastal Center for access, and the US National Science Foundation (DEB-9981654; DEB-0315796) for support.

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Received 17 October 2006; revision accepted 14 March 2007
Editor: Robert Jones