

The effect of Chinese tallow tree (*Sapium sebiferum*) ecotype on soil–plant system carbon and nitrogen processes

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Abstract The EICA hypothesis predicts that shifts in allocation of invasive plants give rise to higher growth rates and lower herbivore defense levels in their introduced range than conspecifics in their native range. These changes in traits of invasive plants may also affect ecosystem processes. We conducted an outdoor pot experiment with Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) seedlings from its native (Jiangsu, China, native ecotype) and introduced ranges (Texas, USA, invasive ecotype) to compare their relative performances in its native range and to examine ecotype effects on soil processes with and without fertilization. Consistent with predictions, plant (shoot and root) mass was significantly greater and leaf defoliation tended to be higher, while the root:shoot ratio was lower for the invasive ecotype relative to the native ecotype. Seasonal amounts of soil–plant system CO₂ and N₂O emissions were higher for the invasive ecotype

than for the native ecotype. Soil respiration rates and N₂O emission increases from fertilization were also greater for the invasive ecotype than for the native ecotype, while shoot-specific respiration rates (g CO₂-C g⁻¹ C day⁻¹) did not differ between ecotypes. Further, soil inorganic N (ammonium and nitrate) was higher, but soil total N was lower for soils with the invasive ecotype than soils with the native ecotype. Compared with native ecotypes, therefore, invasive ecotypes may have developed a competition advantage in accelerating soil processes and promoting more nitrogen uptake through soil–plant direct interaction. The results of this study suggest that soil and ecosystem processes accelerated by variation in traits of invasive plants may have implications for their invasiveness.

Keywords CO₂ · Ecosystem process · EICA · Invasion · N₂O · Soil–plant interaction

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Introduction

The invasion of exotic plants impacts on native species, communities, and ecosystems (e.g., Elton 1958; Lodge 1993; Simberloff 1996). Although the direct impacts of exotic species invasions on community structure and function are often readily apparent and well-studied (Vitousek et al. 1997; Ehrenfeld and Scott 2001), the potential for more subtle alteration of ecosystem processes has received increased attention (e.g., Vitousek 1990; Levine et al. 2002; Ehrenfeld 2003; Dukes and Mooney 2004; Huxman et al. 2004). These studies have demonstrated that the invasion of exotic plants can have far-reaching effects on soil and ecosystem processes (Tilman 2000; Belnap and Phillips 2001; Evans

et al. 2001; Mack et al. 2001; Scott et al. 2001). In general, exotic plants alter soil properties and nutrient cycles through changes in the quantity, quality, and timing of litter inputs (Ehrenfeld et al. 2001; Duda et al. 2003; Allison and Vitousek 2004), or through the short-term soil–plant direct interaction, such as the release of root exudates (Kourtev et al. 2003; Blank and Young 2004; Wolfe and Klironomos 2005). Furthermore, just as differences in the characteristics of invasive species and the native species they replace have important implications for ecosystem processes, variation in traits among ecotypes of invasive species may have similarly important ramifications for the ecosystems they invade.

Presently, no study has examined how variation in traits of invasive plants from native and introduced ranges affects soil and ecosystem processes. It is known, however, that invasive plants often have higher growth rates but lower herbivore defense levels in their introduced range compared to conspecifics in their native range (Blossey and Nötzold 1995; Bossdorf et al. 2005). In physiology, faster growth rates of invasive ecotypes relative to native ecotypes can be attained by higher photosynthetic rates, lower specific respiration rates, or both. On the other hand, soil respiration (soil CO₂ effluxes) consists of two primary components: soil microbial heterotrophic respiration, which occurs during the process of soil organic C decomposition; and root autotrophic respiration, which is closely associated with the mass and metabolic activity of roots. N₂O is produced naturally in the soil microbial processes of nitrification and denitrification. As a result, soil respiration rates and N₂O fluxes could be increased for invasive ecotypes compared to native ecotypes.

Chinese tallow tree (*Sapium sebiferum* L. Roxb., Euphorbiaceae, synonyms include *Triadica sebifera*, henceforth “*Sapium*”) aggressively displaces native plants and forms monospecific stands in the southeastern USA (Bruce et al. 1997; Siemann and Rogers 2003a). Consistent with the evolution of increased competitive ability hypothesis (EICA hypothesis), recent investigations have suggested that *Sapium* has evolved a reduction in defense allocation and an increase in allocation to growth and reproduction in response to the absence of herbivores in the introduced range (Siemann and Rogers 2001, 2003b, 2003c; Rogers and Siemann 2004, 2005). This allocation shift may alter physiological traits between native and invasive ecotypes of *Sapium*. Relative to native ecotypes, on the other hand, the faster growth rates of invasive ecotypes may accelerate soil processes and increase nitrogen availability (plant-available N) in soils through the soil–plant direct interaction. Thus, we might expect

that native and introduced ecotypes differ in a number of traits that may influence ecosystem processes.

Our objective was to examine the effect of *Sapium* ecotype on shoot-specific respiration rates, soil nitrogen availability, and soil–plant system carbon and nitrogen processes. We also sought to verify that the higher growth rates and greater herbivore susceptibility of invasive compared to native ecotypes found in the introduced range (Siemann and Rogers 2001) were also found in the native range. Thus, we conducted a common garden study with native and invasive ecotypes in Jiangsu, China, in which we compared the relative performances of *Sapium* ecotypes and measured soil nitrogen contents and seasonal emissions of CO₂ and N₂O.

Materials and methods

Seeds

In November and December 2003, seeds were hand-collected from naturalized *Sapium* trees in Texas, USA (henceforth “invasive ecotype”) and in Jiangsu, China (henceforth “native ecotype”). Seeds were collected from many different trees within each region. Seeds of both native and introduced *Sapium* trees were planted in separate Conetainers (Stuewe and Sons, Corvallis, OR, USA) in an unheated shadehouse at Nanjing Agricultural University, Nanjing, Jiangsu, China (31°52'N, 118°50'E) in December 2003. The Conetainers were filled with soil taken from the top 20 cm of the profile in winter wheat croplands at Jiangsu Academy of Agricultural Sciences in Nanjing, where *Sapium* trees are naturalized in uncultivated areas. The experimental soil was classified as hydromorphic, consisting of 29% sand, 16% silt and 55% clay with an initial pH (H₂O) of 6.7. Soil nitrogen and organic carbon contents were 0.98 and 9.36 mg g⁻¹, respectively. Seeds in the soil went through the whole winter season and germinated throughout March. The small seedlings grew in the Conetainers for about four weeks until they had secondary leaves, at which time they were transplanted into pots.

Pot experiment

A 120-day pot experiment was performed in the shadehouse at Nanjing Agricultural University, Jiangsu, China, where several *Sapium* trees were growing in the surrounding vicinity. At the beginning of May, 36 *Sapium* seedlings of native ecotypes (CH) and 36 *Sapium* seedlings of invasive ecotypes (US), together

with the original substrate soil, were individually transplanted into 6.50-l tree pots filled with topsoil from the wheat croplands. We measured stem height and recorded leaves on each seedling before transplanting. Pots were randomly assigned *Sapium* ecotype (CH and US) and fertilizer application (F and C) treatments to establish a full two-factorial experimental design. The pots had extremely small drain holes and when watering the pots we made sure that only minimal amounts of water passed through them in order to minimize leaching of nitrogen. Nitrogen fertilizer for each ecotype (CH-F and US-F) was applied as urea at a rate of 6 g pot⁻¹ just before seedling transplanting, and the pots with no nitrogen addition were used as the controls for two different ecotypes of *Sapium* (CH-C and US-C). We used two subexperiments: one to measure soil–plant system CO₂ and N₂O effluxes (“Efflux Experiment” hereafter), and one to partition shoot respiration and soil respiration (“Respiration Experiment” hereafter). In the Efflux Experiment, seedlings of native and invasive ecotypes of a similar height were selected for treatment combinations with six replicates, and thus 24 pots were used to routinely measure soil–plant system CO₂ and N₂O emissions. In the Respiration Experiment, we used the remaining 48 pots to partition soil respiration and shoot dark respiration from whole soil–plant system CO₂ emissions. On June 25, July 29, August 16, and September 1, 2004, we measured soil respiration and shoot dark respiration rates on three replicate pots for the two ecotypes and two fertilizer treatments. On the August 16th sampling date, we collected fresh soil samples from the 12 pots from which seedlings were harvested in order to measure inorganic N (plant-available N, NH₄⁺N + NO₃⁻ – N) and total N content. Ammonium (NH₄⁺N) and nitrate (NO₃⁻ – N) contents were determined by a continuous flow analyzer (Skalar, Breda, The Netherlands) method. Total nitrogen in the soil was determined by the Kjeldahl (TKN) method.

CO₂ and N₂O emissions

In the Efflux Experiment, soil–plant system CO₂ and N₂O fluxes from 24 pots were measured from May 8 to September 5 twice a week in the first month and once a week thereafter. In the Respiration Experiment, a cutting-plant method was used to quantitatively partition soil respiration and shoot dark respiration from the whole soil–plant system CO₂ emissions; this was performed four times over the whole season. The cutting-plant method was described in detail by Zou et al. (2005). In this method, soil–plant system CO₂ fluxes and soil CO₂ effluxes were measured before and after

the shoots were removed at the soil surface, respectively. Soil CO₂ effluxes reflected soil respiration, consisting of root autotrophic respiration and soil heterotrophic respiration of rhizosphere microbes and microbes in the remaining volume of soils. Shoot dark respiration (CO₂ effluxes from shoots) was therefore quantified as the difference between soil–plant system CO₂ fluxes and soil CO₂ effluxes, since plant photosynthesis in an opaque chamber was interrupted while gas sampling (Zou et al. 2004, 2005). This difference in CO₂ fluxes (mg CO₂–C m⁻² h⁻¹) was divided by the corresponding shoot mass and then translated into shoot-specific respiration rate, which was expressed in terms of a respiratory coefficient (R_D , g CO₂–C g⁻¹ C day⁻¹), i.e., CO₂–C emission in grams of dark respiration per gram of shoot dry matter carbon per day. For each sample, shoots were harvested and roots were gently washed from the soil. Shoots and roots were dried at 60 °C for three days and weighed separately. These mass data were also used to outline the seasonal dynamics of plant growth.

The fluxes of CO₂ and N₂O emissions were simultaneously measured by static opaque chamber–gas chromatograph (GC) method. This method has been previously performed to investigate CO₂ and N₂O emissions in agricultural ecosystems (Huang et al. 2002, 2004; Zou et al. 2004, 2005) and more details on the method can be found in Huang et al. (2002). Between 0800 and 1000 LST, gas samples were taken from the headspace in an open-bottomed cylindrical chamber. The chamber was 100 cm high and wrapped in a layer of sponge and aluminum foil to minimize temperature changes during the period of sampling. While taking gas samples, the chamber was placed over the vegetation, with the rim of the chamber fitted into the groove of the pot. Carbon dioxide and N₂O mixing ratios were detected by a modified gas chromatograph (4890D, Agilent, Palo Alto, CA, USA) with an electron capture detector (ECD) and a hydrogen flame ionization detector (FID) (Wang and Wang 2003; Huang et al. 2004). Carbon dioxide was separated by one stainless steel column (2 m length and 2.2 mm inner diameter) packed with 50–80-mesh Porapak Q. Afterwards hydrogen reduced CO₂ to CH₄ in a nickel catalytic converter at 375 °C, and CH₄ was detected by the FID. Nitrous oxide was separated by two stainless steel columns (column 1 with length 1 m and inner diameter 2.2 mm, column 2 with length 3 m and inner diameter 2.2 mm) packed with 80–100 mesh Porapak Q, and detected by the ECD. The oven was operated at 55 °C, the FID at 200 °C and the ECD at 330 °C, respectively. Flux was determined from the slope of the mixing ratio changes in the three samples, taken 0,

10 and 20 min after chamber closure. The air temperature inside the chamber was recorded for each set of emission measurements. Average CO₂ and N₂O fluxes and their standard deviations were calculated from six or three replicates in two subexperiments, respectively. Seasonal amounts of CO₂ and N₂O emissions were sequentially accumulated from the emissions between every two adjacent intervals of the measurements. Before plant harvesting, we took a final measurement of stem height from ground surface to the terminal bud and recorded the total leaves and average percentage of surface area damaged per leaf. On September 5, shoots and roots were harvested, dried at 60 °C for three days and weighed separately to estimate plant masses and the root:shoot ratios of invasive and native ecotypes.

Data analyses

Stem height growth was calculated as [(final height – initial height)/initial height], where initial height was measured on May 8 prior to the initiation of the experiment and final height was measured on September 5 prior to plant harvest. Percent defoliation of leaf surface area was square-root-transformed for analysis. For each ecotype of *Sapium*, fertilizer-induced N₂O emission was quantified as [100% × (seasonal amount of N₂O–N from fertilized pots – seasonal amount of N₂O–N from unfertilized pots)/fertilized N]. In the Respiration Experiment, soil respiration rates and shoot respiration rates on the different dates were normalized with $Q_{10}=2.0$ at the reference temperature 20 °C to describe their seasonal dynamics. The value of Q_{10} was estimated from the diurnal dynamics of the CO₂ fluxes of the soil–plant system ($Flux = 50.4e^{0.071T}$, $Q_{10}=2.04$) and soil respiration ($Flux = 34.1e^{0.065T}$, $Q_{10}=1.92$) with temperature (T) during the midseason of seedling growth. We used a two-way factorial analysis of variance (ANOVA, SYSTAT 10.0, SPSS Inc., Cary, NC, USA) to compare plant mass, root:shoot ratio, stem growth, number of leaves, percent leaf

defoliation, soil nitrogen content (NH₄⁺-N, NO₃⁻-N, inorganic N and total N) and seasonal amounts of soil–plant system CO₂ and N₂O emissions between the different experimental treatments. We also performed a three-way factorial ANOVA to test for the effect of fertilizer, *Sapium* ecotype, and plant development stage (i.e., sampling time) on soil respiration and shoot-specific respiration rates.

Results

Performance of native and invasive ecotypes

Regardless of fertilizer treatment, the shoot mass, root mass, and total plant mass of the invasive ecotypes harvested at the end of the “Effluxes Experiment” were significantly higher than those of the native ecotypes (Table 1, Fig. 1a). Adding nitrogen increased shoot mass, root mass, and total mass of *Sapium* seedlings, but there was no significant interaction of ecotype with fertilizer, suggesting a similar response of the two ecotypes to nitrogen addition (Table 1, Fig. 1a). With nitrogen addition, root mass and shoot mass of the invasive ecotype were, on average, 55 and 75% greater than those of the native ecotype, respectively. Without nitrogen addition, they were, on average, 24 and 45% higher for the invasive ecotype than the native ecotype, respectively (Fig. 1a). However, the root:shoot ratio of *Sapium* seedlings were significantly lower for the invasive ecotype than for the native ecotype (Table 1). Nitrogen addition significantly decreased the root:shoot ratios of seedlings of both native and invasive ecotypes (Table 1). Moreover, plant mass harvested on different dates in the “Respiration Experiment” also suggested that both root and shoot growth rates tended to be greater for invasive ecotypes than native ecotypes, with or without nitrogen addition (Fig. 2a,b). However, the root:shoot ratio of the invasive ecotype was generally lower than that of the native ecotype when compared for a specific time or plant size (Fig. 2c,d).

Table 1 A two-way analysis of variance (ANOVA) for shoot mass, root mass, total mass, and root:shoot ratio of *Sapium sebiferum*

Factor	df	Shoot biomass			Root biomass			Total biomass			Root:shoot ratio		
		SS	F	P	SS	F	P	SS	F	P	SS	F	P
E	1	137	12.8	0.002	7	5.9	0.02	205	11.8	0.003	0.03	11.6	0.003
F	1	94	8.8	0.008	4	3.4	0.08	137	7.9	0.011	0.02	9.5	0.006
E × F	1	19	1.8	0.19	2	1.3	0.27	32	1.8	0.19	0.00	0.5	0.50
Model	3	251	7.8	0.001	12	3.5	0.03	373	7.1	0.002	0.06	7.2	0.002
Error	20	214			23			348			0.05		

Plant mass harvested in the “Effluxes Experiment” on 5 September 2004

F fertilizer treatment, E *Sapium* ecotype

Fig. 1a–d Mean (± 1 SE, $n=6$) root mass, shoot mass and total mass (a), stem height growth rate (b), the number of leaves per seedling (c), and the square-root transformed percent defoliation per leaf (d) of *Sapium sebiferum* in relation to fertilizer and ecotype. Data were collected at the end of the “Effluxes Experiment.” CH native ecotype, US invasive ecotype, C control treatment of no fertilization, F fertilizer treatment

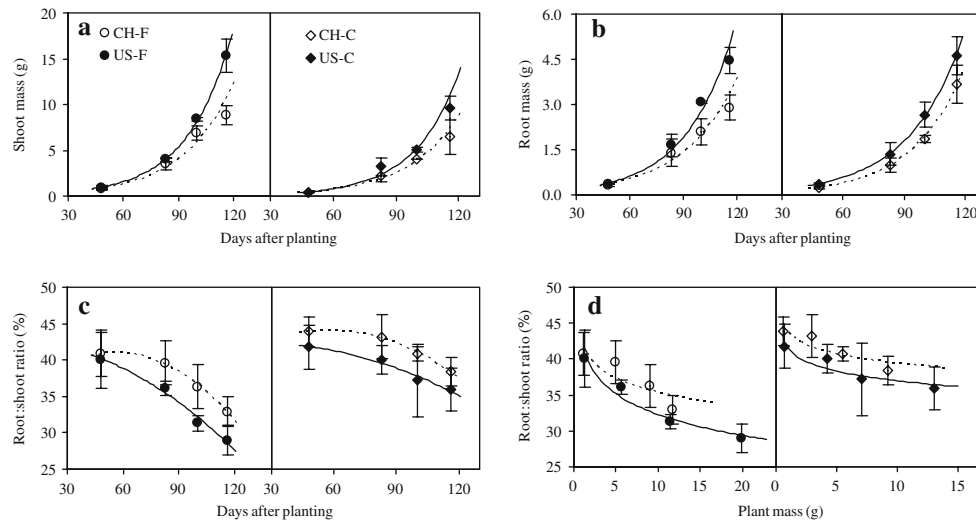
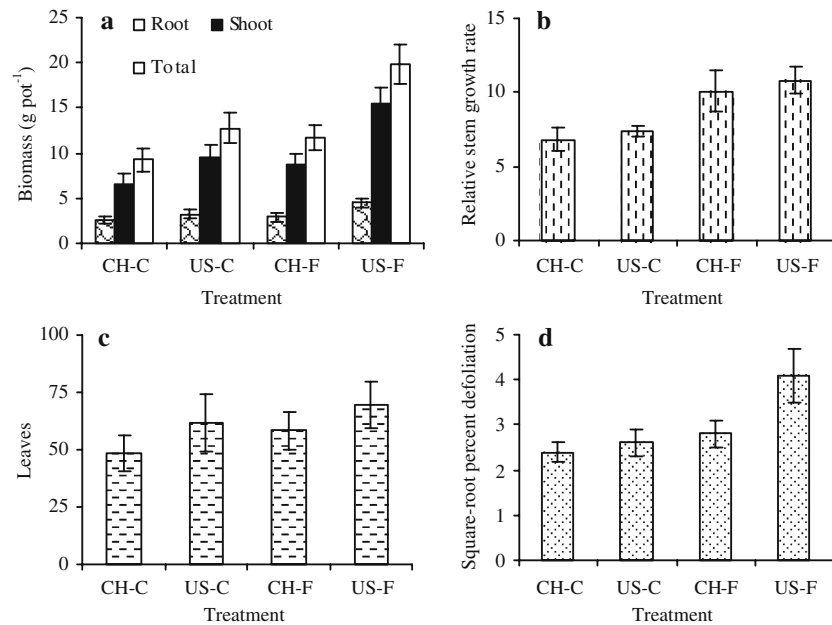


Fig. 2a–d Seasonal dynamics of root (a) and shoot (b) mass (mean ± 1 SE, $n=3$) of invasive and native ecotypes of *Sapium sebiferum*, and root:shoot ratio of two ecotypes when compared at a common time (c) and at a common plant size (d, mass), respec-

tively. Masses were harvested in the “Respiration Experiment.” CH native ecotype, US invasive ecotype, C control treatment of no fertilization, F fertilizer treatment

Stem height growth rate increased with nitrogen application ($F_{(1,20)}=11.8$, $P=0.003$), but it was not affected by *Sapium* ecotype ($F_{(1,20)}=0.4$, $P=0.54$) or by their interaction ($F_{(1,20)}=0.002$, $P=0.97$, Fig. 1b). Total number of leaves per seedling was not significantly affected by ecotype ($F_{(1,20)}=1.5$, $P=0.24$), fertilizer ($F_{(1,20)}=0.8$, $P=0.38$) or their interaction ($F_{(1,20)}=0.01$, $P=0.91$, Fig. 1c). However, leaf damage tended to be greater for the invasive ecotype than for the native ecotype ($F_{(1,16)}=4.0$, $P=0.06$) and was greater for seedlings growing in the nitrogen treatments ($F_{(1,16)}=5.9$, $P=0.03$, Fig. 1d). No significant interaction between ecotype

and fertilizer on leaf damage was found ($F_{(1,16)}=1.8$, $P=0.20$).

Soil nitrogen

Fertilizer application increased soil inorganic N (ammonium and nitrate) content (Table 2, Fig. 3). Invasive ecotypes had significantly higher soil inorganic N than the native ecotype of *Sapium* (Table 2). However, total N content in the soil was significantly lower for the invasive ecotype relative to the native ecotype of *Sapium* (Table 2, Fig. 3). Thus, N uptake by

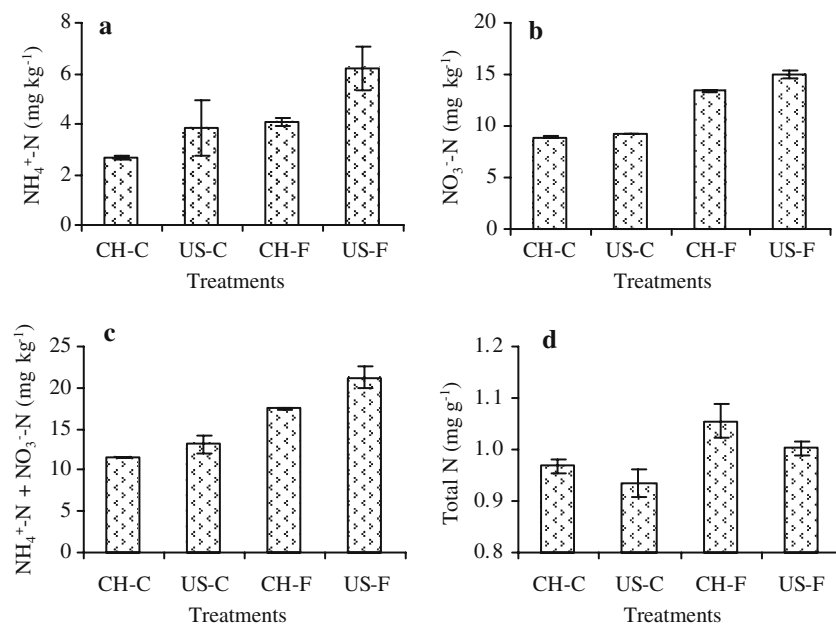
Table 2 A two-way analysis of variance (ANOVA) for soil ammonium ($\text{NH}_4^+\text{-N}$, mg kg^{-1}), nitrate ($\text{NO}_3^- \text{-N}$, mg kg^{-1}), plant-available nitrogen ($\text{NH}_4^+ + \text{NO}_3^-$) and total nitrogen (N, %) contents

Factor	df	$\text{NH}_4^+\text{-N}$			$\text{NO}_3^- \text{-N}$			$\text{NH}_4^+\text{-N} + \text{NO}_3^- \text{-N}$			Total N		
		SS	F	P	SS	F	P	SS	F	P	SS	F	P
E	1	8	15.7	0.004	3	91.3	<0.0001	21	28.9	0.0007	1	10.6	0.01
F	1	10	20.3	0.002	80	2392.5	<0.0001	148	203.7	<0.0001	2	33.9	0.0004
E × F	1	1	1.3	0.29	1	40.0	0.0002	4	5.3	0.05	0	0.5	0.48
Model	3	19	12.4	0.002	84	841.3	<0.0001	172	79.3	<0.0001	2	15.0	0.001
Error	8	4			0			6			0		

Soil nitrogen content measured on 16 August 2004

F fertilizer treatment, E *Sapium* ecotype

Fig. 3a–d Mean (± 1 SE, $n=3$) soil ammonium ($\text{NH}_4^+\text{-N}$, **a**), nitrate ($\text{NO}_3^- \text{-N}$, **b**), inorganic nitrogen ($\text{NH}_4^+ \text{-N} + \text{NO}_3^- \text{-N}$, **c**), and total nitrogen (**d**) as affected by *Sapium sebiferum* ecotype and fertilizer application. Measurements were made on 16 August 2004. CH native ecotype, US invasive ecotype, C control treatment of no fertilization, F fertilizer treatment



seedlings of the invasive ecotype from soil was greater than uptake by the native ecotype since the decrease in soil N over time was mainly due to consumption by *Sapium* seedlings. No significant interaction between fertilizer and ecotype on soil $\text{NH}_4^+\text{-N}$ and total N was found, suggesting that increases in soil $\text{NH}_4^+\text{-N}$ and total N by urea application were not affected by *Sapium* ecotypes. However, a significant interactive effect on soil $\text{NO}_3^- \text{-N}$ and total plant available N suggests that soil nitrification was increased more for the invasive ecotype than for the native ecotype when $\text{NH}_4^+\text{-N}$ was increased from urea hydrolyzation in soil (Table 2, Fig. 3).

CO₂ emissions

Seasonal amounts of soil–plant system CO₂ emissions were significantly higher for the invasive ecotype than for the native ecotype (Table 3). Nitrogen application tended to increase soil–plant system CO₂ emission

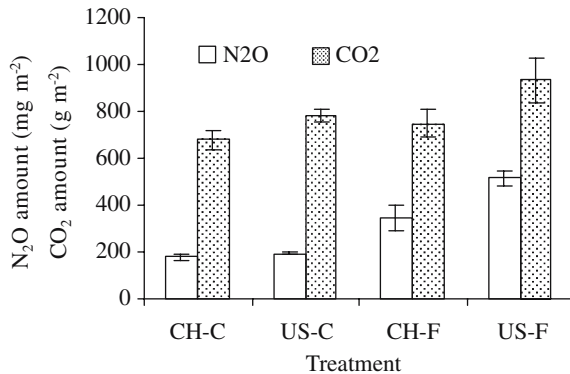
(Table 3, Fig. 4). There was no interaction of ecotype with fertilizer (Table 3), suggesting that the effect of ecotype on CO₂ emissions did not significantly vary with fertilizer addition. Soil–plant system CO₂ fluxes of the invasive ecotype averaged 363.5 mg CO₂ m⁻² h⁻¹ with nitrogen addition, and 304.6 mg CO₂ m⁻² h⁻¹ without nitrogen addition. They were, on average, 25 and 15% greater than those of the native ecotype, respectively (Fig. 4).

Soil CO₂ effluxes gradually increased over the growing season (Table 4, Fig. 5a). On average, soil respiration rate increased from 65.6 mg CO₂ m⁻² h⁻¹ for the CH-C treatment on June 25 to 146.8 mg CO₂ m⁻² h⁻¹ for the US-F treatment on September 1 (Fig. 5a). Soil respiration rate generally increased with nitrogen addition during the experiment and tended to be greater for the invasive ecotype than for the native ecotype (Table 4). When nitrogen was added, soil respiration rate of the invasive ecotype was, on average, 20% higher on August 16 and 16% higher on September 1

Table 3 A two-way ANOVA for seasonal amounts of soil–plant system CO₂ and N₂O emissions

Factor	df	CO ₂			N ₂ O		
		SS	F	P	SS	F	P
E	1	124,762	5.8	0.03	52,463	8.4	0.01
F	1	74,170	3.5	0.08	354,367	56.4	<0.0001
E × F	1	9,672	0.5	0.51	35,014	5.6	0.03
Model	3	208,605	3.2	0.04	441,844	23.5	<0.0001
Error	20	427,399			125,583		

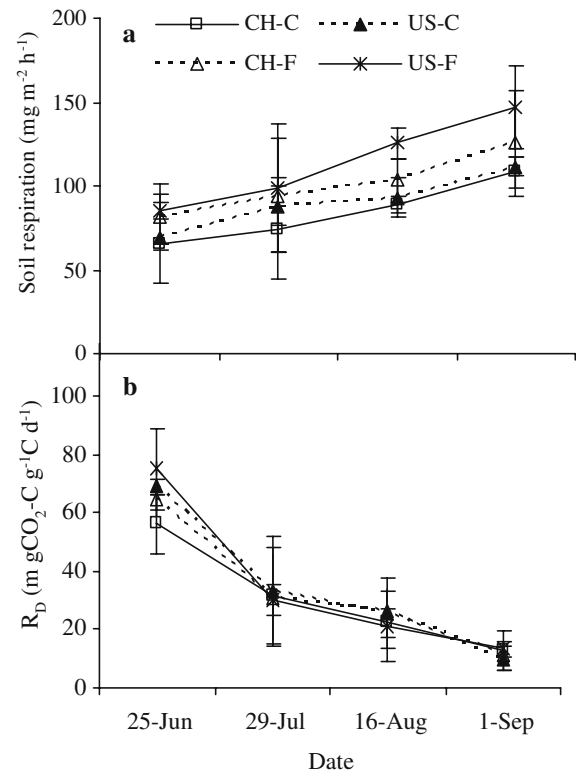
F fertilizer treatment, E *Sapium* ecotype

**Fig. 4** Seasonal amounts of soil–plant system CO₂ and N₂O emissions (mean ± 1 SE, n=6) in the native and invasive ecotypes of *Sapium sebiferum*. CH native ecotype, US invasive ecotype, C control treatment of no fertilization, F fertilizer treatment**Table 4** A three-way ANOVA for soil respiration (mg CO₂ m⁻² h⁻¹) and shoot-specific respiration rates (mg CO₂-C g⁻¹ C day⁻¹)

Factor	df	Soil respiration rate			Shoot-specific respiration rate		
		SS	F	P	SS	F	P
E	1	1,295	3.0	0.09	0.1	0.4	0.54
F	1	4,961	11.5	0.002	0.1	0.3	0.60
T	3	14,952	11.5	<0.001	20.2	81.3	<0.0001
E × F	1	32	0.8	0.39	0.1	0.5	0.50
E × T	3	73	0.1	0.98	0.4	1.4	0.26
F × T	3	270	0.2	0.89	0.2	0.9	0.47
E × F × T	3	687	0.5	0.67	0.1	0.3	0.80
Model	15	22,569	3.5	0.001	20.9	16.8	<0.0001
Error	32	13,815			2.7		

F fertilizer treatment, E *Sapium* ecotype, T time

than the native ecotype. There were no interactive effects of treatments on soil respiration rate (Table 4). Shoot-specific respiration rate decreased gradually throughout the growing season (Table 4, Fig. 5b). In general, shoot-specific respiration rate was not significantly affected by *Sapium* ecotype, fertilizer addition over the whole season, or interactions of any factors (Table 4).

**Fig. 5a–b** Seasonal dynamics of soil respiration rate (a) and shoot-specific respiration rate (R_b , b) (mean ± 1 SE, n=3)

N₂O emissions

Nitrogen addition significantly increased whole-season N₂O emissions (Table 3, Fig. 4). N₂O emissions from soil–plant system were higher for the invasive ecotype than for the native ecotype (Table 3, Fig. 4). A significant interaction of ecotype with fertilizer on N₂O emission suggested that the effect of fertilizer on N₂O emission was influenced by *Sapium* ecotype (Table 3). In contrast with nonfertilized controls, nitrogen addition increased N₂O emissions by 94% for the native ecotype and 199% for the invasive ecotype, which accounted for 0.26% and 0.54% of the applied N, respectively. The highest N₂O emission occurred in the invasive ecotype of *Sapium* when nitrogen was added (Fig. 4).

Discussion

The EICA hypothesis predicts that plants have higher growth rate and more herbivore susceptibility of invasive ecotypes than native ecotypes when they are grown in the native range. Recently, common garden studies have been widely used to test for the EICA hypothesis (Bossdorf et al. 2005). In the present study,

we found that shoot mass, root mass, and the total mass of the invasive ecotype of *Sapium* were significantly greater than those of the native ecotype despite the tendency for invasive *Sapium* seedling leaves to be damaged to a greater degree by herbivores than native *Sapium* seedlings when grown in the native range (Fig. 1a,d). The seasonal dynamics of plant growth outlined in Fig. 2 also show that plant growth rate was generally higher for the invasive ecotype than for the native ecotype. Additionally, the difference in root:shoot ratio between native and invasive ecotypes when compared at a common plant size suggests that relatively more mass was allocated to photosynthetic tissues for the invasive ecotype, and relatively more mass to root growth for the native ecotype. The higher growth rate and greater herbivory damage of the invasive ecotype of *Sapium*, therefore, supports the EICA hypothesis and our previous results suggesting that *Sapium* has evolved a reduction in defense allocation and an increase in allocation to growth in response to the absence of herbivores in the introduced range (Siemann and Rogers 2001, 2003b, 2003c; Rogers and Siemann 2004, 2005). Nevertheless, variation in allocation of *Sapium* between native and invasive ecotypes deserves further investigation.

Besides the allocation shifts, faster growth of the invasive ecotype, from the general perspective of plant physiology, could have been attained through a higher photosynthetic rate, a lower specific respiration rate, or both. However, we found no significant difference in shoot-specific respiration rate between two ecotypes of *Sapium* over the whole season (Table 4, Fig. 5b). Therefore, it is likely that the more rapid growth of the invasive ecotype was caused by a higher photosynthetic rate rather than a lower specific respiration rate. It is evident that some invasive plants outperformed the co-occurring native species by maximizing photosynthesis (e.g., Baruch and Goldstein 1999; Durand and Goldstein 2001; McDowell 2002; Nagel and Griffin 2004); however, DeWalt et al. (2004) found no difference in photosynthetic rates between native and introduced ecotypes of the invasive tropical shrub *Clidemia hirta* (Melastomataceae). Although we cannot conclusively demonstrate the mechanism that underlies the differences in the growth rates of *Sapium* ecotypes in this study, some variations in traits of invasive *Sapium* clearly affected soil processes.

The soil–plant direct interaction may play an important role in the impact of exotic plant invasions on soil and ecosystem processes. In this pot study, seedlings of two ecotypes were initially planted in identical soils, so any differences in the soils at the end of experiment were due to the short-term soil–plant interaction. The

combination of higher inorganic N (ammonium and nitrate) and lower total N (organic plus inorganic) in soil associated with the invasive ecotype means that organic N must have decreased in these soils relative to those associated with native ecotypes. This could have been caused by leaching of organic N from the pots or by increased net mineralization (N mineralization minus N immobilization). We assume that leaching losses were minimal in this study because pots were watered sparingly and leaching would be more likely to deplete inorganic N, which is more soluble in water. Thus, organic N net mineralization rates were likely greater for soils associated with the invasive ecotype than for those associated with the native ecotype. The hypothesis of greater N mineralization rates *per se* is supported by the result that soil respiration (soil organic C mineralization) rates were higher for soils associated with the invasive ecotype relative to those associated with the native ecotype of *Sapium*. On the other hand, the interaction of ecotype with fertilizer on soil NO_3^- -N and inorganic N (NH_4^+ -N + NO_3^- -N) suggests that soil nitrification may also have been increased more for the invasive ecotype than for the native ecotype of *Sapium* when urea hydrolyzation released NH_4^+ -N in the soil. This is partially supported by the significant interaction between ecotype and fertilizer on N_2O emissions, since N_2O is produced primarily through nitrification in aerobic soil environments. However, higher N_2O emissions suggest that soil denitrification may also be increased for the invasive ecotype in comparison with the native ecotype of *Sapium*.

On the other hand, plant growth and the ability of a plant to compensate for leaf damage are strongly influenced by availability of soil resources (Coley et al. 1985; Davis et al. 2000; Davis and Pelsor 2001; Elberse et al. 2003). In the present study, a significantly lower soil total N content in pots with invasive ecotypes reflects the fact that overall uptake of N by invasive ecotypes was more than the uptake by native ecotypes. This could have been caused by a greater amount of plant-available N in the soil (Fig. 3). In this short-term pot study, increased soil nitrogen availability may have, in turn, contributed to the invasive ecotype outperforming the native ecotype of *Sapium* seedlings. If the increased soil inorganic nitrogen associated with the invasive ecotype of *Sapium* is primarily available to closely associated roots, this may contribute to *Sapium*'s invasive success as well.

Furthermore, alteration of soil processes and plant physiological traits have changed ecosystem CO_2 emissions from native and invasive ecotypes of *Sapium*. In this study, ecosystem CO_2 was significantly higher for the invasive ecotype than for the native ecotype

(Table 3, Fig. 4). Higher ecosystem CO₂ emission for the invasive ecotype can be induced by two components: one is CO₂ effluxes from shoot respiration associated with larger shoot mass at a similar respiratory coefficient (Figs. 1a, 5b), and the other is higher soil respiration rates (Table 4, Fig. 5a). Compared with the native ecotype, the larger root mass of the invasive ecotype is predicted to produce more exudates in the rhizosphere, which are readily available to soil microorganisms. The increased availability of nitrogen and carbon may provide higher energetic material or substrate that stimulates greater soil microorganism growth and activity in the invasive ecotype than in the native ecotype. Indeed, the soil respiration rate tended to be higher in the invasive ecotype relative to the native ecotype.

Nitrogen application significantly increased N₂O emissions for both native and invasive ecotypes. However, the interactive effect of ecotype with fertilizer suggested that the increase in N₂O emissions due to additional nitrogen for the invasive ecotype was significantly higher than for the native ecotype (Table 3, Fig. 4). Nitrous oxide is produced naturally in soils through the microbial processes of nitrification and denitrification. It has been shown that soil N₂O and CO₂ fluxes are simultaneously increased by additional C and N inputs (Aulakh et al. 1991; Flessa and Beese 1995; Huang et al. 2004). Compared with the native ecotype, higher soil NH₄⁺ and NO₃⁻-N provided more substrate for the invasive ecotype. Besides the availability of inorganic nitrogen (NO₃⁻, NH₄⁺) in the soil, soil bacterial community composition is recognized as being another factor important to N₂O emissions. While soil inorganic nitrogen was abundant due to nitrogen addition in this study, N₂O fluxes may also depend upon the soil bacterial community, which is involved in the processes of nitrification and denitrification. The soil–plant direct interaction may change soil bacterial abundance and community composition and therefore increase soil nitrification and denitrification rates in soils. Hawkes et al. (2005) found that exotic grasses can significantly change the abundance and composition of the soil-nitrifying community compared to native grasses.

While much research has documented the effect of exotic plant invasion or species diversity on ecosystem processes due to changes in the quality, quantity and timing of litter inputs (Ehrenfeld et al. 2001; Duda et al. 2003; Allison and Vitousek 2004; Hobbie and Gough 2004), the soil–plant direct interaction may also affect ecosystem processes (Kourtev et al. 2003; Blank and Young 2004; Wolfe and Klironomos 2005). The results of this study suggest that shifts in allocation between native and invasive ecotypes of *Sapium* altered soil

carbon and nitrogen processes, which created a positive feedback that caused the performance of the seedlings of invasive ecotypes to outperform those of native ecotypes. Similarly, the results from a three-month greenhouse incubation of exotic species and co-occurring native species showed that plant species can significantly alter soil microbial communities and soil processes through the short-term soil–plant interaction (Kourtev et al. 2003). The authors attributed differences in available N in the soil and soil mineralization and nitrification to the differences in nitrogen uptake between the three plant species and changes in the activity of microorganisms in the soil (Kourtev et al. 2003).

Conclusions

Overall, *Sapium* seems to have evolved to be a faster-growing, more herbivore-tolerant plant in response to low herbivore loads in its invasive range. The present study suggests that these allocation shifts of invasive ecotypes have altered plant physiological characteristics in ways that have altered soil C and N processes such as mineralization. These changes led to an increase in soil nitrogen availability that may have contributed to the invasive ecotype outperforming the native ecotype of *Sapium* in this pot experiment. Moreover, these changes have subsequently increased ecosystem CO₂ and N₂O emissions. If the allocation shifts and the types of invasive ecotype trait variation shown for *Sapium* are common, such ecosystem-level effects may be found for other invasive species. Therefore, a positive feedback that promotes soil carbon and nitrogen cycling created by the soil–plant direct interaction may have implications for exotic plant invasiveness.

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