



Comparisons of plastic responses to irradiance and physiological traits by invasive *Eupatorium adenophorum* and its native congeners

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ABSTRACT

To explore the traits contributing to invasiveness of *Eupatorium adenophorum* and to test the relationship between plasticity of these traits and invasiveness, we compared *E. adenophorum* with its two native congeners at four irradiances (10%, 23%, 40%, and 100%). The invader showed constantly higher performance (relative growth rate and total biomass) across irradiances than its native congeners. Higher light-saturated photosynthetic rate (P_{\max}), respiration efficiency (RE), and nitrogen (PNUE) and water (WUE, at 40% and 100% irradiances only) use efficiencies contributed directly to the higher performance of the invader. Higher nitrogen allocation to, stomatal conductance, and the higher contents of leaf nitrogen and pigments contributed to the higher performance of the invader indirectly through increasing P_{\max} , RE, PNUE and WUE. The invader had consistently higher plasticity only in carotenoid content than its native congeners in ranges of low (10–40%), high (40–100%) and total (10–100%) irradiances, contributing to invasion success in high irradiance by photo protection. In the range of low irradiances, the invader had higher plasticity in some physiological traits (leaf nitrogen content, nitrogen contents in bioenergetics, carboxylation and in light-harvesting components, and contents of leaf chlorophylls and carotenoids) but not in performance, while in the ranges of high or total irradiances, the invader did not show higher plasticity in any variable (except Car). The results indicated that the relationship between invasiveness and plasticity of a specific trait was complex, and that a universal generalization about the relationship might be too simplistic.

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Introduction

General-purpose genotype hypothesis predicts that invasive alien plant species occupy wide geographic areas with diverse habitats and outperform co-occurring natives through plastic responses to environment conditions (phenotypic plasticity) without genetic

changes (Baker, 1974; Sultan, 1995; Weber and Schmid, 1998; Parker et al., 2003; Li and Feng, 2009). Although higher plasticity has been found for some invasive plants compared with natives (Williams et al., 1995; Pattison et al., 1998; Niinemets et al., 2003; Gurevitch et al., 2008), the relationship between invasiveness and plasticity is still not clear (Daehler, 2003; Burns and Winn, 2006). Phenotypic plasticity may facilitate a genotype to tolerate a broad range of environments and to increase performance in multiple environments (Callaway et al., 2003). Invasive alien plants inevitably encounter novel abiotic and biotic environments after introduction and/or during following range expansion, which they do not meet in their native ranges. Phenotypic plasticity is crucial for invasive plants to colonize new environments, increasing ecological breadth and potentially available resources, facilitating performance and invasions especially at changing environments (Sultan and Bazzaz, 1993; Ghalambor et al., 2007).

Most early studies focused on comparing plasticity of single traits between invasive plants and comparators. However, the response of performance to environment changes is achieved through interactions among physiological and morphological

Abbreviations: Car, leaf carotenoid content (g m^{-2}); Chl, leaf chlorophyll content (g m^{-2}); G_s , stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$); N_A , total leaf nitrogen content (g m^{-2}); N_B , nitrogen content in bioenergetics (g m^{-2}); N_C , nitrogen content in carboxylation (g m^{-2}); N_L , nitrogen content in light-harvesting components (g m^{-2}); P_{\max} , light-saturated photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); P_T , plasticity to total irradiance; P_H , plasticity to high irradiances; P_L , plasticity to low irradiances; PNUE, photosynthetic nitrogen use efficiency ($\mu\text{mol g}^{-1} \text{s}^{-1}$); R_d , dark respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); RE, respiration efficiency ($\mu\text{mol} \mu\text{mol}^{-1}$); RGR, relative growth rate ($\text{mg g}^{-1} \text{d}^{-1}$); SLA, specific leaf area ($\text{cm}^2 \text{mg}^{-1}$); WUE, water use efficiency ($\mu\text{mol mol}^{-1}$).

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traits. For example, area-based nitrogen (N) content (N_A) and leaf N allocated to carboxylation (N_C) and bioenergetics (N_B) of the photosynthetic processes increase with increasing irradiance, while specific leaf area (SLA) and leaf N allocated to light-harvesting components (N_L) decrease (Niinemets and Tenhunen, 1997; McDowell, 2002; Niinemets et al., 2003; Baltzer and Thomas, 2007; Feng, 2008). These plastic responses to irradiance increase light capture ability (decrease leaf construction cost) at low irradiance and increase light-saturated photosynthetic rate (P_{max}) and photosynthetic N use efficiency (PNUE) at high irradiance, contributing to high performance.

Richards et al. (2006) proposed three phenotypic plasticity strategies to characterize invasive plant performance. One strategy is expressed as phenotypic plasticity assists the invader to maintain constant performance advantage over natives across an environment gradient. The second strategy depicts cases where phenotypic plasticity enables performance to be higher under certain environmental conditions. The third strategy is the combination of the above two strategies. Hulme (2008) concluded that the plasticity strategy depends strongly on the regions of environment gradient. However most studies examined only a partial subset of the full environment range experienced by plant species, and drew inaccurate conclusions about the role of plasticity in biological invasions.

Eupatorium adenophorum Sprengel (Asteraceae) [Syn. *Ageratina adenophora* (Sprengel) R.M. King and H. Robinson] is native to Central America but a globally noxious invasive perennial forb throughout the subtropics. It spread into Yunnan Province from Burma in the 1940s, and now it has invaded in six provinces in Southwest China (Zheng et al., 2009). It can replace native species and even forms dense monoculture in diverse habitats. Phylogeny has an evident effect on the results of paired comparisons, while most studies compared unrelated invasive and native plants at one or few environments (but see Feng, 2008). Relative performance of invasive and native plants is environment-dependent, and comparisons between related invasive and native plants in diverse environments are more informative in elucidating plant traits contributing to invasiveness (McDowell, 2002; Daehler, 2003; Grotkopp and Rejmánek, 2007; Feng, 2008). Irradiance is one of the important resources for plants; survival, growth, and reproduction all depend on it. Competition for light is an important factor influencing some plant invasions (D'Antonio et al., 2001; Standish et al., 2001). Yamashita et al. (2000) found when transferred from shade to a sunny environment, invasive *Bischofia javanica* have a rapid photosynthetic acclimation in existing shade leaves by minimizing photo inhibition, and a rapid deployment of new sun leaves with high photosynthetic capacity. Our previous study has showed that *E. adenophorum* has higher performance than native congeners (*Eupatorium japonicum* L. and *Eupatorium heterophyllum* DC) in diverse irradiances (Zheng et al., 2009). However, the physiological mechanisms associated with the higher performance of *E. adenophorum* were unclear, and the relationship between plasticity of physiological traits and invasiveness was also not tested. So, in this study, we compared *E. adenophorum* with its two native congeners at four irradiances. We first explored which physiological traits contributed to the higher performance of the invader. Then we analyzed the relationships between invasiveness and plasticity of these physiological traits and performance.

Materials and methods

Study site and species

This study was carried out at Xishuangbanna Tropical Botanical Garden (21°56'N, 101°15'E) of Chinese Academy of Sciences located in Mengla County, Yunnan Province, southwest China. The

mean annual temperature is 21.7 °C in this area. The mean temperature in the hottest month (July) is 25.3 °C, and that in the coolest month (January) is 15.6 °C. The average annual precipitation is 1557 mm, with a dry period lasting from November to April.

Eupatorium japonicum L. and *Eupatorium heterophyllum* DC are native perennial forbs with similar stature (1–2 m tall) as *Eupatorium adenophorum* in many provinces in China. They have sympatric distributions with *E. adenophorum*, and also occur in various habitats such as understory, edge of forests, shrubs, and grasslands (Feng et al., 2007; Feng, 2008). According to field observations, the two congeners usually distribute in partial shade environments, and they are rare in the environments with low or high irradiances. *E. adenophorum* has high density in 40–100% irradiances, while it is still common in the environments from 20% to 40% irradiances. It can be found even at 5% irradiance. The seeds of the studied species were collected at two sites 40 km apart from each other around Kunming, Yunnan Province.

Irradiance treatment

Seeds of studied species were sown at a seedbed in a greenhouse in December 2006. In February, 2007, when the seedlings of the species were approximately 10 cm tall, similar sized seedlings were transplanted singly into 10 dm³ plastic pots. The pots were filled with equal proportions of river sand and the top layer of forest soil. All seedlings were grown at 23% irradiance for two weeks. The seedlings of each species were divided randomly into four groups, and each group (25 seedlings) was grown at one of the four irradiances (10%, 23%, 40% and 100%), respectively. Seedlings were watered with tap water (~2 dm³) every other day and fertilized with complex fertilizer (15% N, 15% P and 15% K) at 2 g per pot in March.

The irradiances used in this study were created by covering shade houses with different layers of black nylon shade netting (Tongchuang, Beijing, China), including no netting to create 100% irradiance. The relative irradiance in each shade house was estimated by comparing the integrated photosynthetic photon flux density (PPFD) in it during a clear day with the house with no netting (Appendix A). Quantum sensors and a Li-1400 Datalogger (Li-Cor, Lincoln, NE) were used to measure PPFD. For reducing potential differences within each shade house and among shade houses for other environment factors except irradiance, four big shade houses (each is 6.5 m × 5.0 m × 2.5 m) were constructed in an open site, and the lower 20 cm of each shade house remained open to facilitate airflow. In order to avoid position effect, the pots were arranged in center parts of each house, and rerandomized fortnightly within each shade house throughout the experiment. As in most experiments that control irradiance (e.g. Pattison et al., 1998; Baltzer and Thomas, 2007), we had no replication of the shade house with similar irradiance, and the seedlings in each shade house were used as replicates to do statistical analyses.

Measurements

In March and June of 2007, five seedlings per species and treatment were harvested, oven-dried at 80 °C for 48 h, and total biomass (including roots, which were collected by carefully rinsing soil from roots) of each seedling was measured, respectively. Relative growth rate (RGR) was calculated as: $RGR = (\ln W_2 - \ln W_1) / \Delta t$, where W_1 and W_2 represent total biomass of each sample seedling at the initial and final harvests, respectively, and Δt indicates the days between the initial and final harvest.

Before the final harvest, photosynthetic response to intercellular CO₂ concentration (C_i) was determined on new fully expanded leaves (the fifth or sixth leaf from top) of four individuals per

species and treatment using a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE) with well watered to minimize the stomatal patchiness (Terashima, 1992). We first conducted a preliminary measurement to explore the saturating light level and CO₂ concentration of each species under each house. Then, under a saturating level of PPFD (1600 μmol m⁻² s⁻¹ in 40–100% irradiances, 1000 μmol m⁻² s⁻¹ in 10–23% irradiances), net photosynthetic rate (P_n) was measured at 380, 300, 260, 220, 180, 140, 110, 80 and 50 μmol mol⁻¹ CO₂ in the reference chamber. Relative humidity of the air in the leaf chamber was controlled at ≈70%, leaf temperature at 30 °C. The constant values of stomatal conductance (G_s), C_i and P_n of each sample leaf were recorded after 180 s under each PPFD and CO₂ step. Photosynthetic rate measured at 380 μmol mol⁻¹ CO₂ and saturating PPFD was P_{max} ; dark respiration rate (R_d) was determined after 300 s under 0 μmol m⁻² s⁻¹ PPFD and 380 μmol mol⁻¹ CO₂. Afterwards, light- and CO₂-saturated photosynthetic rate (P'_{max}) was detected after 500 s under saturating PPFD and 1500 μmol mol⁻¹ CO₂. Before measurement, each sample leaf was illuminated with saturating PPFD provided by the LED light source of the equipment for 5–30 min to achieve fully photosynthetic induction. No photo inhibition occurred during the measurements.

Leaf discs (excluding main vein) were taken from each sample leaf and oven-dried at 60 °C for 48 h. N_A was determined with a Vario MAX CN Element Analyser (Elementar Analysensysteme GmbH, Hanau, Germany). Leaf chlorophyll (Chl) and carotenoid (Car) contents were measured following the method of Lichtenthaler and Wellburn (1983). The same leaf of each sample plant was used if possible for measurements of photosynthesis, Chl, Car, SLA, and N_A , but in some cases, similar leaves were used for some measurements. SLA was calculated as the ratio of leaf area to mass; PNUE as the ratio of P_{max} to N_A ; water use efficiency (WUE) as the ratio of P_{max} to G_s ; respiration efficiency (RE) as the ratio of P_{max} to R_d .

Maximum carboxylation rate (V_{cmax}) was derived from P_n – C_i curves. P_n – C_i curve was fitted with linear equation ($P_n = kC_i + i$) within 50–200 μmol mol⁻¹ C_i , where k was carboxylation efficiency (CE), $-i/k$ was equal to CO₂ compensation concentration (Γ^*) in the absence of mitochondria respiration (Laisk et al., 2005), which was very low under irradiation. Maximum electron transport rate (V_{cmax}) was calculated with light- and CO₂-saturated photosynthetic rate. The contents of Rubisco and cytochrome (cyt) f were calculated with V_{cmax} and J_{max} , respectively. N allocated to carboxylation (N_C) and to bioenergetics (N_B) was calculated with the contents of Rubisco and cyt f , respectively. N content in light-harvesting components (N_L) was calculated with chlorophyll content (C_C). The theories and calculations are presented in detail by Niinemets and Tenhunen (1997), Loustau et al. (1999), Warren and Adams (2004), Kitaoka and Koike (2004), Feng and Fu (2008) and Feng et al. (2008). V_{cmax} , J_{max} , N_C , N_B and N_L were calculated according to following equations.

$$V_{cmax} = \frac{k[C_i + K_c(1 + O/K_o)]^2}{\Gamma^* + K_c(1 + O/K_o)} \quad (1)$$

$$J_{max} = \frac{4(P'_{max} + R_d)(C_i + 2\Gamma^*)}{C_i - \Gamma^*} \quad (2)$$

$$N_C = \frac{V_{cmax}}{6.25 \times V_{cr}} \quad (3)$$

$$N_B = \frac{J_{max}}{8.06 \times J_{mc}} \quad (4)$$

$$N_L = \frac{C_C}{SLA \times C_B} \quad (5)$$

where K_c and K_o are 469.8 μmol mol⁻¹ and 456.2 μmol mol⁻¹ at 30 °C, respectively, and O is 210 mmol mol⁻¹ (Niinemets and

Tenhunen, 1997). V_{cr} and J_{mc} are 32.76 μmol CO₂ g⁻¹ Rubisco s⁻¹ and 182.33 μmol electrons μmol⁻¹ cyt f s⁻¹ at 30 °C, respectively; C_B is 2.15 mmol g⁻¹; 6.25 (g Rubisco g⁻¹ nitrogen in Rubisco) is the conversion coefficient between nitrogen content and protein content in Rubisco; and 8.06 (μmol cyt f g⁻¹ nitrogen in bioenergetics) is the conversion coefficient between cyt f and nitrogen in bioenergetics (Niinemets et al., 1998).

Valladares et al. (2000) calculated plasticity index as the ratio of the difference between the maximum and the minimum means of each variable among irradiances to the maximum mean. In this study, the maximum mean of each variable was replaced by each value of sample individual at the corresponding irradiance. In this way, we could obtain as many plasticity indices for each species and variable as the number of sample individuals at the corresponding irradiances and test for the differences among the three studied species in plasticity index of each variable. In order to test the differences in plasticity among different regions of full environment range, the plasticity of each trait in total irradiances (10–100%, P_T), in high irradiances (40–100%, P_H), and in low irradiances (10–40%, P_L) were calculated, respectively.

Statistical analyses

A two-way ANOVA was used to test for the effects of species, irradiance, and their interactions on each variable evaluated in this study. One-way ANOVAs (Tukey–Kramer test) were used to test for the differences among species at the same irradiance, the differences among irradiances for the same species in each variable, and the differences among species in plasticity (P_T , P_H and P_L). A one-way ANCOVA was used to test for the difference between *E. adenophorum* and its native congeners in the correlation between each pair of the variables presented in Figs. 2–4, with species category (invasive vs. native) as a fixed factor, and variables indicated by y - and x -axes as dependent variable and covariate, respectively. If the difference was significant, we then tested for the significance of the correlation (Pearson correlation, two-tailed) for the invasive and native species separately; otherwise, we pooled data from all species to test for the significance of correlation. All analyses were carried out using SPSS 17.0 (SPSS Inc., Chicago, IL).

Results

Species (except for R_d) and irradiance (except for WUE) significantly affected all variables evaluated in this study (Table 1). The interactions between species and irradiance were also significant for most of the variables, indicating genetic differences in plasticity for these variables, i.e. the patterns of the differences among species in these variables were different at different irradiances. For example, *E. adenophorum* compared with its native congeners showed significantly higher WUE only at 40% and 100% irradiances (Fig. 1D). The invader had lower SLA than the natives at 10–40% irradiances but not at 100% irradiance (Fig. 1B). Similarly, the difference between the invasive and native species in G_s was not significant at 100% irradiance although the invader had higher values than the natives at 10% and 23% irradiances (Fig. 1G). However, the invader had consistently higher P_{max} , PNUE, RE, N_A , N_C , N_B , N_L , Chl, Car, RGR and total biomass across irradiances than the natives (Fig. 1). P_{max} , PNUE, R_d , G_s , N_A , N_C , N_B , N_L , Chl, Car, RGR (except *E. japonicum* at 100% irradiance) and total biomass (except *E. japonicum* at 100% irradiance) increased, while SLA decreased with increasing irradiance for all studied species (Fig. 1).

The invader had significantly higher P_T in Car but lower P_T in SLA, R_d , G_s , N_A and RGR than the natives (Table 1). The invader was not significantly different from the two natives in P_T of P_{max} , RE, PNUE, WUE, N_C , N_B , N_L , Chl and total biomass (Table 1). In high irradiances

Table 1

Effects of species ($n=3$), irradiance ($n=4$) and their interactions on each variable according to a two-way ANOVA and the differences in plasticity in response to range of total irradiances among invasive *Eupatorium adenophorum* and its native congeners according to a one-way ANOVA (Tukey–Kramer test).

Variable	F-value			Plasticity index in range of total irradiance		
	Species, S	Irradiance, I	I × S	<i>E. adenophorum</i>	<i>E. heterophyllum</i>	<i>E. japonicum</i>
P_{max}	175.74***	187.84***	2.74*	0.43b	0.52a	0.47ab
RE	87.91***	5.84**	1.89	0.13a	0.18a	0.17a
PNUE	41.77**	13.36***	0.36	0.13a	0.18a	0.13a
WUE	6.50**	2.22	7.46***	0.19a	0.22a	0.19a
R_d	1.48	93.64***	2.50*	0.36b	0.49a	0.53a
G_s	39.69***	62.52***	3.76**	0.30b	0.50a	0.53a
N_A	236.88***	629.35***	10.05***	0.35b	0.41a	0.39a
N_C	83.37***	154.10***	6.34**	0.52a	0.48ab	0.43b
N_B	176.21***	387.07***	6.97**	0.50b	0.56a	0.50b
N_L	109.61***	28.53**	2.34	0.24ab	0.17b	0.29a
Chl	77.45***	22.53**	1.61	0.24a	0.16b	0.29a
Car	161.68***	270.63***	26.21***	0.65a	0.53b	0.54b
RGR	33.82***	295.49***	3.23**	0.636b	0.748a	0.758a
Biomass	34.15***	66.92***	8.44***	0.95a	0.95a	0.96a
SLA	49.84***	327.13***	8.20***	0.62b	0.71a	0.71a

RGR, P_{max} and total biomass have been published in Zheng et al. (2009).

Different letters in the same row indicate significant differences among species ($P<0.05$). Car, leaf carotenoid content in $g\ m^{-2}$; Chl, leaf chlorophyll content in $g\ m^{-2}$; G_s , stomatal conductance in $mol\ m^{-2}\ s^{-1}$; N_A , total leaf nitrogen content in $g\ m^{-2}$; N_B , nitrogen content in bioenergetics in $g\ m^{-2}$; N_C , nitrogen content in carboxylation in $g\ m^{-2}$; N_L , nitrogen content in light-harvesting components in $g\ m^{-2}$; P_{max} , light-saturated photosynthetic rate in $\mu mol\ m^{-2}\ s^{-1}$; PNUE, photosynthetic nitrogen use efficiency in $\mu mol\ g^{-1}\ s^{-1}$; R_d , dark respiration rate in $\mu mol\ m^{-2}\ s^{-1}$; RE, respiration efficiency in $\mu mol\ \mu mol^{-1}$; RGR, relative growth rate in $mg\ g^{-1}\ d^{-1}$; SLA, specific leaf area in $cm^2\ mg^{-1}$; WUE, water use efficiency in $\mu mol\ mol^{-1}$.

* $P<0.05$.

** $P<0.01$.

*** $P<0.001$.

(40–100%), *E. adenophorum* showed significantly higher plasticity in Car but lower plasticity in P_{max} , G_s , N_A , N_C , N_B and total biomass than the native congeners (Table 2). There were no distinct differences for P_H in RE, PNUE, WUE, R_d , N_L , Chl, SLA and RGR between *E. adenophorum* and the natives (Table 2). In low irradiances (10–40%), *E. adenophorum* showed higher plasticity in N_A , N_C , N_B , N_L , Car and Chl but lower plasticity in RGR than the natives (Table 2). Significant differences were not found for P_L in P_{max} , RE, PNUE, WUE, R_d , G_s , SLA and total biomass between *E. adenophorum* and the native congeners (Table 2). For *E. adenophorum*, plasticity indices of all variables (except RE) were lower in high irradiances than in low irradiances, whereas for natives, plasticity indices of G_s , N_A , N_C , N_B , N_L and Chl were higher in high irradiances than in low irradiances (Table 2). Plastic response of performance (biomass and RGR) was weaker for all species in high irradiances than in low irradiances (Table 2).

Total biomass and RGR increased linearly with increasing P_{max} and PNUE (Fig. 2). P_{max} increased significantly with increasing N_C , N_B , N_A , R_d and G_s , but decreased with increasing SLA (Fig. 3). The

invader had higher P_{max} at the same value of R_d , N_A or G_s (only at high values), consistent with its higher RE, PNUE, and WUE (at 40% and 100% irradiances) (Fig. 3C–E). With the increase of N_C , N_B and N_A , PNUE increased significantly and was significantly higher for the invader than for the natives at the same value of N_C , N_B or N_A (Fig. 4).

Discussion

Higher P_{max} , RE, PNUE and WUE may contribute to invasiveness of the invader

High RGR is an important trait for alien invasive plants (Burns, 2004; Burns and Winn, 2006; Grotkopp and Rejmánek, 2007). The higher P_{max} of *E. adenophorum* compared with its native congeners may contribute to its higher RGR through increasing net assimilation rate (NAR), one of the determinants of RGR. The positive correlation between NAR and P_{max} has been found (Feng et al., 2007). In this study, we also found the positive correlations

Table 2

The differences in plasticity in response to ranges of high and low irradiances among invasive *Eupatorium adenophorum* and its native congeners according to one-way ANOVA (Tukey–Kramer test).

Variable	Plasticity index in high irradiances (40–100%)			Plasticity index in low irradiances (10–40%)		
	<i>E. adenophorum</i>	<i>E. heterophyllum</i>	<i>E. japonicum</i>	<i>E. adenophorum</i>	<i>E. heterophyllum</i>	<i>E. japonicum</i>
P_{max}	0.18b	0.34a	0.33a	0.31a	0.26ab	0.20b
RE	0.08ab	0.18a	0.04b	0.05a	0.13a	0.17a
PNUE	0.00a	0.05a	0.00a	0.13a	0.12a	0.13a
WUE	0.00b	0.16a	0.09ab	0.19a	0.22a	0.12a
R_d	0.10b	0.19ab	0.29a	0.29a	0.16b	0.25ab
G_s	0.15b	0.36a	0.39a	0.17a	0.21a	0.22a
N_A	0.18b	0.31a	0.33a	0.21a	0.15b	0.09b
N_C	0.18b	0.35a	0.28a	0.41a	0.19b	0.20b
N_B	0.22b	0.39a	0.35a	0.36a	0.27b	0.22b
N_L	0.08b	0.14b	0.28a	0.13a	0.01b	0.04b
Car	0.27a	0.11b	0.13b	0.52a	0.46b	0.47b
Chl	0.12b	0.14b	0.28a	0.13a	0.01b	0.04b
SLA	0.25b	0.41a	0.35ab	0.49b	0.50b	0.56a
RGR	0.02b	0.13a	0.10ab	0.63c	0.71b	0.76a
Biomass	0.06a	0.38a	0.30a	0.94a	0.92b	0.96a

Different letters in the same row indicate significant differences ($P<0.05$) among species. Abbreviations as in Table 1.

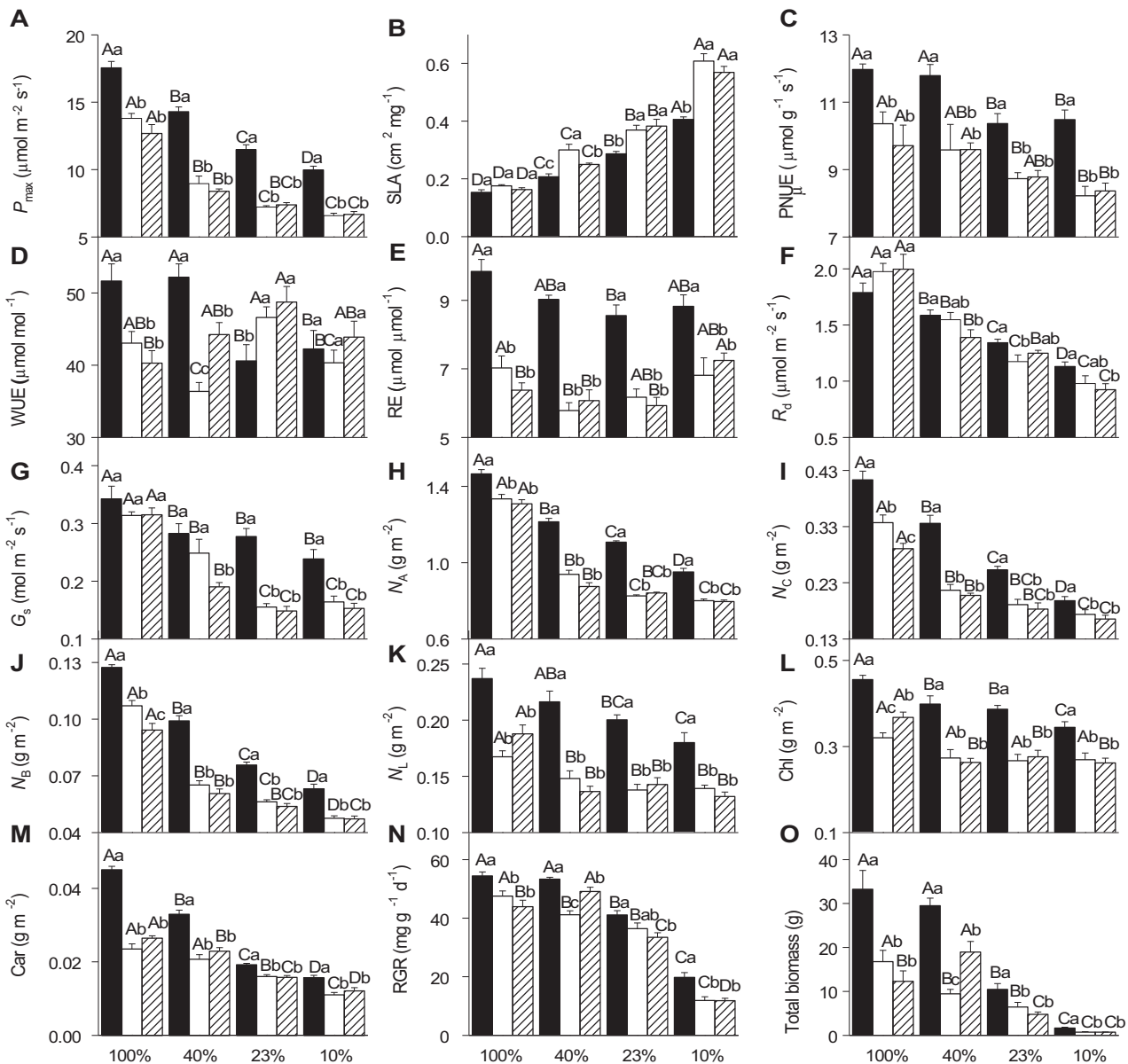


Fig. 1. Differences among invasive *Eupatorium adenophorum* (black bars) and native *E. heterophyllum* (open bars) and *E. japonicum* (hatched bars) grown at different irradiances. Mean \pm SE ($n = 5$ for RGR and biomass; $n = 4$ for others). Different small and capital letters indicate significant differences ($P < 0.05$) among species at the same irradiance and among irradiances for the same species, respectively. Abbreviations as in Table 1.

RGR, P_{max} and total biomass have been published in Zheng et al. (2009).

between RGR, total biomass and P_{max} (Fig. 2A and C). Higher RGR of *E. adenophorum* can facilitate growth of ramets and branches, increasing crown area and total leaf area, which might give the invader a competitive advantage by shading native plants (Feng et al., 2007).

Respiration is an important physiological process for plants, providing metabolic intermediates and energy directly for maintenance of cellular activities (maintenance respiration) and growth (growth respiration) (Amthor, 1989). Positive correlation between P_{max} and R_d has been found in many studies (Fig. 3D; Pattison et al., 1998; McDowell, 2002). On the other hand, respiration may also consume organic matter, impairing biomass accumulation. *E. adenophorum* showed significantly higher RE, while its R_d was not significantly different from natives (Fig. 1E and F). These results indicated that the invader could accumulate more photosynthates than natives at the same value of respiration cost (Fig. 3D), contributing to higher RGR and therefore to invasiveness.

The positive correlations between RGR, biomass and PNUE indicated that the higher PNUE of the invader may contribute to its higher biomass and RGR (Fig. 2B and D), which was consistent with previous studies (Field et al., 1983; Lambers and Poorter, 1992; Schieving and Poorter, 1999). In addition, the invader also showed significantly higher WUE at 40% and 100% irradiances (Fig. 1D), breaking the trade-off between PNUE and WUE (DeLucia and Schlesinger, 1991; McDowell, 2002; Feng et al., 2008).

Traits contributing to the higher P_{max} , RE, PNUE and WUE of the invader

P_{max} was positively correlated with N_A , N_C and N_B (Fig. 3A–C). The result may be due to the fact that N_C and N_B are positively correlated with the maximum rates of carboxylation and electron transport, which influence P_{max} directly (Feng et al., 2008). Our results indicated that the higher N_A , N_C and N_B at all irradiances

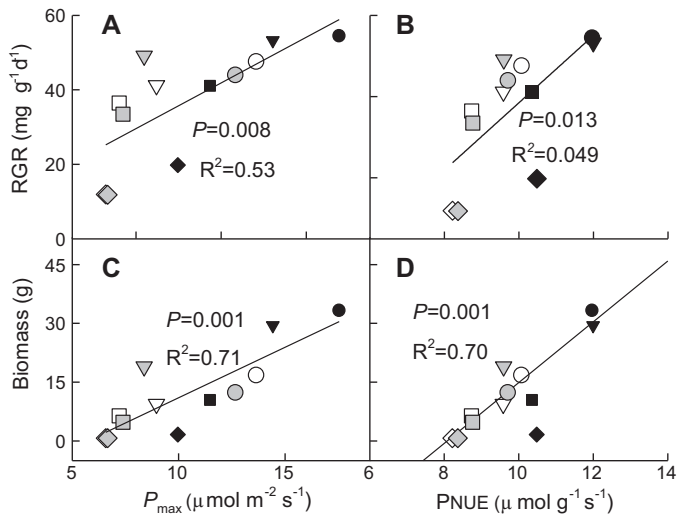


Fig. 2. RGR and biomass as a function of (A and C) P_{max} and (B and D) PNUE in invasive *Eupatorium adenophorum* (filled symbols) and native *E. heterophyllum* (open symbols) and *E. japonicum* (grey symbols) grown at 10% (diamonds), 23% (squares), 40% (triangles) and 100% (circles) irradiances. Mean value of each variable was given ($n=5$ for RGR and biomass; $n=4$ for others). Abbreviations as in Table 1.

contributed to the higher P_{max} of the invader. Higher G_s of the invader (Fig. 1G) may also contribute to its higher photosynthetic rate through increasing CO_2 supply (Fig. 3E). The higher chloroplast pigment contents of the invader (Fig. 1L and M) may contribute to its higher RGR and total biomass through increasing light capture and photosynthetic rate under low PPFD.

Lower N_A contributes to a higher PNUE in invasive plants compared with natives (McDowell, 2002; Niinemets et al., 2003). However, in this study, N_A is higher for *E. adenophorum* than native congeners (Fig. 1H). In addition, PNUE increased linearly with N_A (Fig. 4C). Compared with native congeners, *E. adenophorum* allocated more fractions of leaf nitrogen to carboxylation, bioenergetics and light-harvesting components, contributing to higher PNUE of *E. adenophorum* (Fig. 4A and B). The higher RE and WUE (at 40% and 100% irradiances only) of the invader might also be associated with its higher P_{max} and therefore with its higher nitrogen allocation to photosynthesis, because its R_d and G_s were not lower than its native congeners (Fig. 1F and G).

Defensive chemicals, cell walls, cell nucleus, and other cellular components also account for some proportions of leaf N although most of leaf N is allocated to photosynthesis (Evans, 1989; Feng et al., 2009). Increasing N allocation to these components may decrease N allocation to photosynthesis. For example, high-SLA plants compared with low-SLA plants allocate lower fractions of

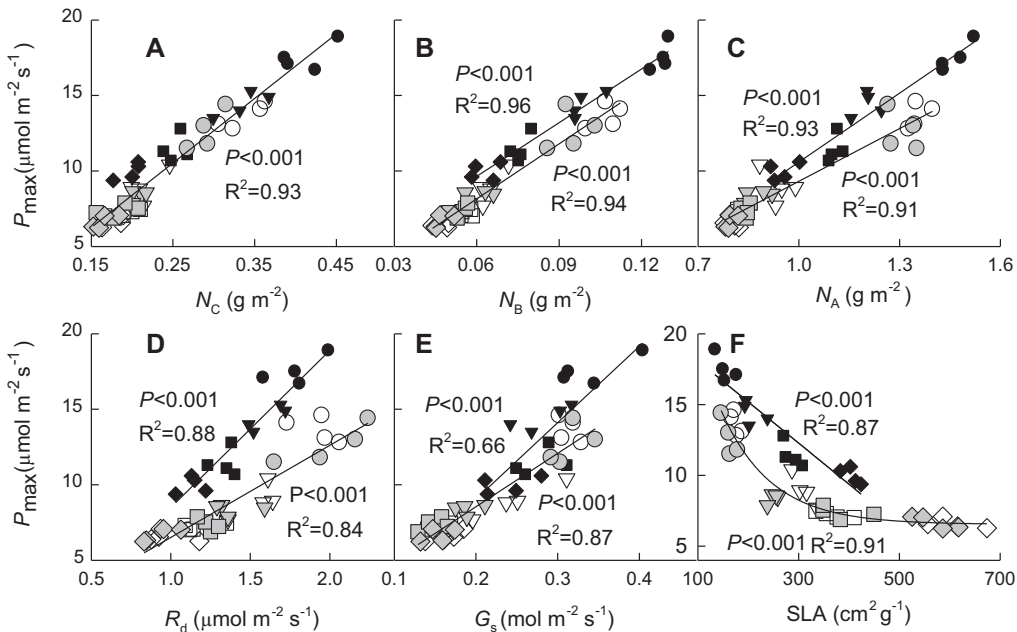


Fig. 3. P_{max} as a function of (A) N_c , (B) N_b , (C) N_A , (D) R_d , (E) G_s , (F) C_i and (G) SLA in invasive *Eupatorium adenophorum* (filled symbols) and native *E. heterophyllum* (open symbols) and *E. japonicum* (grey symbols) grown at 10% (diamonds), 23% (squares), 40% (triangles) and 100% (circles) irradiances. Abbreviations as in Table 1.

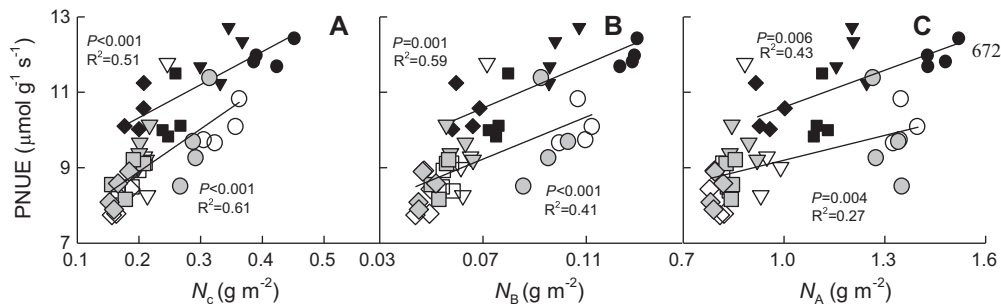


Fig. 4. PNUE as a function of (A) P_c , (B) P_b and (C) N_A in invasive *Eupatorium adenophorum* (filled symbols) and native *E. heterophyllum* (open symbols) and *E. japonicum* (grey symbols) grown at 10% (diamonds), 23% (squares), 40% (triangles) and 100% (circles) irradiances. Abbreviations as in Table 1.

leaf N to cell walls and higher fractions of leaf N to photosynthesis, showing tradeoffs between N allocation to cell walls and photosynthesis (Onoda et al., 2004; Takashima et al., 2004; Feng et al., 2009). However, *E. adenophorum* did not show higher SLA than natives (Fig. 1B), indicating that the tradeoffs between N allocation to cell walls and photosynthesis could not explain its higher N allocation to photosynthesis.

Plasticity and invasiveness

Car was the only variable in which the invader showed consistently higher plasticity index than its native congeners in ranges of low (10–40%), high (40–100%) and total (10–100%) irradiances (Tables 1 and 2). The results indicated that the relative increment in Car with increasing irradiance was higher for the invader than for its native congeners, contributing to photo protection. Many studies found that carotenoids have a role in thermal dissipation of excessive energy (ref). Thus, the high plasticity of Car may contribute to invasion success of the invader in high irradiances.

Invasive *E. adenophorum* had significantly higher plasticity indices in N_A , N_C , N_B , N_L , Chl and Car than its native congeners in range of low irradiances but not in ranges of high and total irradiances (except Car) (Tables 1 and 2). The results indicated that the relative increments in these variables when irradiance increased from 10% to 40% were higher for the invader than for its native congeners. Consistently, the invader had higher relative increment in P_{max} , as judged by its higher plasticity of P_{max} (not significant compared with *E. heterophyllum*) in range of low irradiances (Table 2). However, the higher relative increment in P_{max} did not result in higher relative increments in performance (RGR and total biomass). In fact, the relative increment in RGR was lower for the invader than for its native congeners, as judged by its lower plasticity index of RGR (Table 2). Similarly, with increasing irradiance, the two native congeners showed higher relative increments in P_{max} , G_s , N_A , N_C , N_B , N_L and Chl in range of high irradiances than in range of low irradiances, as judged by plasticity indices, which also did not lead to higher relative increments in performance (lower plasticity) in range of high irradiances (Table 2). The inconsistent changing trends (plastic responses) of physiological traits and performance were also found in previous studies (Sultan, 1995; Sultan et al., 1998), which may be associated with the differences in plasticity of morphological traits between species or ranges of environments. For example, total leaf area did not increase and even decreased for the natives when irradiance increased from 40% to 100% (Zheng et al., 2009), which may give a possible explanation to the less relative increment in performance in range of high irradiance relative to the range of low irradiances.

Our study showed that the relationship between invasiveness and plasticity of a specific trait was complex. Performance plasticity is achieved by interactions among plasticities of morphological and/or physiological traits. Plastic responses of plants depend on their intrinsic characters, the category and range of target environment. A species may have higher plasticity in some traits than another species in a certain set of environments, but not in other traits, or for the same traits in another set of environments (Sultan, 1995; Sultan et al., 1998; Richards et al., 2006; Hulme, 2008). In addition, plasticity is costly (DeWitt et al., 1998; Avramov et al., 2007), and a greater magnitude of plastic responses does not necessarily translate to greater performance and adaptation (Richards et al., 2006).

Conclusion

The constantly higher P_{max} , RE, PNUE and WUE (at 40% and 100% irradiances) of *E. adenophorum* relative to its native congeners

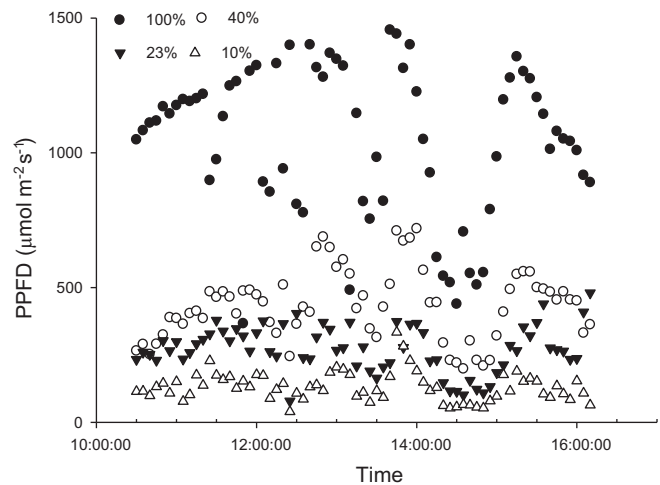


Fig. A1. Photosynthetic photon flux density of each house.

contributed to its higher RGR and total biomass across irradiances. The invader had consistently higher plasticity only in Car than its native congeners in ranges of low (10–40%), high (40–100%) and total (10–100%) irradiances, contributing to invasion success in high irradiance by photo protection. In range of low irradiance, the invader had higher plasticity in some physiological traits (N_A , N_C , N_B , N_L , Chl and Car) but not in performance. The results indicated that the relationship between invasiveness and plasticity of a specific trait was complex. The role of plasticity in invasion success may be different in different environments, and a universal generalization about the relationship might be too simplistic.

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Appendix A.

Fig. A1.

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