Irradiance acclimation, capture ability, and efficiency in invasive and non-invasive alien plant species

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Abstract

We tested the hypothesis that invasive (IN) species could capture resources more rapidly and efficiently than non-invasive (NIN) species. Two IN alien species, *Ageratina adenophora* and *Chromolaena odorata*, and one NIN alien species, *Gynura* sp. were compared at five irradiances. Photon-saturated photosynthetic rate (P_{max}), leaf mass (LMA) and nitrogen content (N_A) per unit area, and photosynthetic nitrogen utilization efficiency (PNUE) increased significantly with irradiance. LMA, N_A, and PNUE all contributed to the increased P_{max}, indicating that both morphological and physiological acclimation were important for the three alien species. Under stronger irradiance, PNUE was improved through changes in N allocation. With the increase of irradiance, the amount of N converted into carboxylation and bioenergetics increased, whereas that allocated to light-harvesting components decreased. The three alien species could adequately acclimate to high irradiance by increasing the ability to utilize and dissipate photon energy and decreasing the efficiency of photon capture. The two IN species survived at 4.5 % irradiance while the NIN species *Gynura* died, representing their different invasiveness. *Ageratina* generally exhibited higher respiration rate (R_D) and N_A. However, distinctly higher P_{max}, PNUE, P_{max}/R_D, or P_{max}/LMA were not detected in the two invasive species, nor was lower LMA. Hence the abilities to capture and utilize resources were not always associated with invasiveness of the alien species.

Additional key words: carbon costs; chlorophyll fluorescence; irradiance; morphology; nitrogen allocation; photosynthesis; photosynthetic nitrogen utilization efficiency.

Introduction

Biological invasions, as a part of global changes (Vitousek *et al*. 1997) severely threaten biodiversity (Lodge 1993) and induce great economic cost (Normile 2004) world wide. Very often, invasive (IN) plants adversely influence species composition, structure, and function of an ecosystem (Vitousek *et al*. 1997, D'Antonio and Kark 2002). Identifying the factors that influence invasions by alien plants is helpful to better predict and control potentially invasive species. Several hypotheses have been proposed to explain why alien IN plants can establish, spread, and eventually dominate communities in their new habitat, for example, the novel weapons hypothesis (Callaway and Ridenour 2004), the enemy release hypothesis and biotic resistance hypothesis (Maron and Vilà 2001), and the genetic shift hypothesis (DeWalt *et al*. 2004). However, the mechanisms that

underlie invasiveness are still not well elucidated despite severe impacts of IN plants and extensive studies on them (Mack 1996, McDowell 2002).

Successful IN species must either use limited resources more efficiently than native species or use them at times when they are unavailable to the latter (Vitousek 1986). Pattison *et al*. (1998) hypothesized that successful IN species should have morphological and physiological traits which could increase photon capture and utilization efficiency. But only few studies have been conducted to test the hypothesis and the results are inconsistent. For instance, photon-saturated photosynthetic rate, P_{max} (Pattison *et al*. 1998, Baruch and Goldstein 1999, Durand and Goldstein 2001) and specific leaf area, SLA (Baruch and Goldstein 1999, Durand and Goldstein 2001) are higher for IN species than for native species, whereas

similar or lower P_{max} (Smith and Knapp 2001, Ewe and Sternberg 2003) and SLA (Pattison *et al*. 1998, Smith and Knapp 2001, McDowell 2002) are also documented for IN species.

A few studies have been conducted to compare the ecology of phylogenetically unrelated IN and native species (but see McDowell 2002, DeWalt *et al*. 2004). While most of these comparative studies focused only on IN alien species (Davis *et al*. 2000), only few of them compared traits of IN aliens with those of less or non-invasive (NIN) aliens (Nijs *et al*. 2004). Discoveries of the traits that are different between IN and NIN species may help understand the mechanisms that allow some exotic species to spread rapidly and dominate communities (Mack 1996, Radford and Cousens 2000, Smith and Knapp 2001). A majority (*ca*. 90 %) of successful alien species is NIN (Williamson and Fitter 1996). They can be established and become persistent but unable to out-compete natives (Rejmanek 2000), suggesting that NIN aliens may share more traits with natives than with IN aliens. In this study, the eco-physiological traits were compared among the IN and NIN aliens which are phylogenetically related, ecologically similar, and sympatric in order to test the hypothesis that IN species could capture resources (photons and CO_2) more rapidly and efficiently than NIN species.

Invasiveness of alien species could be affected by efficiency of photosynthesis (Baruch and Goldstein 1999, Durand and Goldstein 2001). IN species may have a higher ability to capture energy at the minimum cost, which allows more resources for growth or reproduction.

Photosynthetic nitrogen utilization efficiency (PNUE), photosynthetic carbon cost (LMA, leaf mass per unit area, and P_{max}/LMA), and respiration efficiency (RE, P_{max} per unit R_D, respiration rate) represent resource capture rates per unit N investment, per unit carbon investment and cost, respectively. Plants with high PNUE usually have high growth rate (Lambers and Poorter 1992). Maximizing PNUE may be a mechanism for the successful invasion of some alien plant species (Baruch and Goldstein 1999, Durand and Goldstein 2001, McDowell 2002, Ewe and Sternberg 2003). IN species have high potential carbon gain at the same respiration cost (Pattison *et al*. 1998, McDowell 2002). Furthermore, compared with native species successful IN species are generally more tolerant to environmental stresses, and could acclimate to a wider range of environmental conditions (Alpert *et al*. 2000) and use fluctuating resources more effectively (Davis *et al*. 2000). Durand and Goldstein (2001) found that the IN fern exhibits higher ability to acclimate to high irradiance than the native ferns. Based on the results from these studies, we hypothesized that the IN species used in this study would have higher ability to acclimate to irradiance than the NIN species.

The main objectives of this study were to determine (*1*) how the alien species could acclimate to different irradiances in terms of physiology and morphology; (*2*) whether the IN species exhibited higher irradiance acclimation ability than the NIN species; (*3*) whether the IN species exhibited higher resources capture rate and efficiency, *i.e.* higher P_{max}, PNUE, RE, P_{max}/LMA, and lower LMA compared with the NIN species.

Materials and methods

This study was carried out in Xishuangbanna Tropical Botanical Garden (XTBG, 21°56'N, 101°15'E), Chinese Academy of Sciences in Mengla county, Yunnan province, southwest China. The mean annual temperature is 21.7 °C in this area. The mean temperature in July, the hottest month is 25.3 °C, and that in January, the coolest month is 15.6 °C. The average annual precipitation is 1 557 mm with dry period lasting from November to April (Feng *et al*. 2002a).

Three exotic Asteraceous forbs, *Ageratina adenophora* (Sprengel) King and Robinson, *Chromolaena odorata* (L.) King and Robinson, and *Gynura* sp. were studied. The former two, native to Central and South America, have invaded into much of the tropics and subtropics in the world. In China they have invaded into both high and low irradiance environments including roadside, abandoned fields, agricultural fields, pastures, and disturbed forest. They replace native species, affect forest succession, crop and pasture growth. *Gynura* sp., native to Burma, is a less or NIN alien according to Nijs *et al*. (2004), for its impact on recipient habitats is very weak in Xishuangbanna. Hereafter, only generic names are used for the three alien species. Plants were grown at

a fully open site (100 % sunshine) and in four shade houses with 4.5, 12.5, 36.0, and 50.0 % sunshine, respectively.

To obtain similar sized seedlings, seeds of *Ageratina* and *Gynura* were sown in May 2002 and July 2002, respectively, in seedbeds under 36 % irradiance. When the seedlings of the two species were approximately 10 cm tall, uniform seedlings were selected and transplanted singly into 15 000 cm³ pottery pots. Current year seedlings of *Chromolaena* were collected as wildings from field in XTBG and transplanted to the same type of pots. Vigorous and uniform seedlings were chosen from partially shaded site. The pots were filled with equal proportions of river sand and top layer of forest soil. All the seedlings were grown at 36 % irradiance for two weeks, then seedlings of each species were divided into five groups randomly, and one group was grown at one of the five irradiances, respectively. Twenty seedlings of every species grown in each irradiance were randomly positioned in the shade house. Seedlings were watered daily, fertilized monthly with complex fertilizer, and rerandomized within the shade house fortnightly through the experiment. Measurements (five replicates) were

taken after seedlings had grown at their new irradiance for two months.

The diurnal changes of chlorophyll (Chl) fluorescence variables were measured at the intervals of 1.5 h from 07:00 to 18:00 on a clear day, using a portable pulse-modulated fluorometer (*FMS, Hansatech*, UK). First, steady-state fluorescence yield (F_s) from the leaf in its original growth position was measured under natural irradiance with a weak modulating beam. Then the maximum light-adapted fluorescence yield (F_m') was determined by irradiating the sample with a pulse of saturated beam (5 000 $\mu mol\ m^{-2}\ s^{-1}$, 0.7 s). Finally, the minimum light-adapted fluorescence yield (F_0') was recorded after keeping the leaf sample in the darkness for 10 s, in the second half of the dark duration the leaf was irradiated by far-red beams. Afterwards, the minimum and maximum fluorescence yields (F_0 and F_m) were detected for the leaf dark-adapted for at least 15 min. According to Bilger and Björkman (1990), the actual photochemical efficiency of photosystem 2 (PS2) in the light (Φ_{PS2}) and the non-photochemical quenching coefficient (NPQ) were calculated as

$$\Phi_{PS2} = (F_m' - F_s)/F_m' \tag{1}$$
$$NPQ = (F_m/F_m' - 1) \tag{2}$$

where F_m was the value measured at dawn. The response of NPQ to photosynthetic photon flux density (PPFD) was determined by irradiating the leaf with "cold light" of different PPFD for 15 min. The "cold light" was provided by several metal halide lamps hanging above a plexiglass water bath with flowing tap water in it. Φ_{PS2} and NPQ were used as indicators of photoinhibition of photosynthesis and thermal dissipation (Feng *et al.* 2002a).

Photosynthetic responses to PPFD and to intercellular CO_2 concentration (C_i) were determined with the *Li-6400* Portable Photosynthesis System (*LI-Cor*, Lincoln, NE, USA). Conditions in leaf chamber were controlled automatically by the equipment, with 60 % relative humidity and 30 °C of leaf temperature. Photosynthetic responses to PPFD were measured under 360 $\mu mol\ mol^{-1}\ CO_2$ using 15 different PPFD. Photosynthetic responses to C_i were measured under 1 500 $\mu mol\ m^{-2}\ s^{-1}$ PPFD using 400, 350, 300, 250, 200, 150, 100, and 50 $\mu mol\ mol^{-1}\ CO_2$ in the reference chamber. Net photosynthetic rate (P_N) was recorded when the leaf was balanced for 200 s under each light and CO_2 step. Finally, photon- and CO_2-saturated photosynthetic rate (P_{max}), which is closely associated with photosynthetic electron chain (Laisk *et al.* 2005), was detected after 400 s under 1 500 $\mu mol\ m^{-2}\ s^{-1}$ PPFD and 1 200 $\mu mol\ mol^{-1}\ CO_2$. Prior to the measurement, the leaf was irradiated by the artificial "cold light" at 1 500 $\mu mol\ m^{-2}\ s^{-1}$ for 30 min in order to achieve fully photosynthetic induction.

Compensation (CI) and saturation (SI) irradiances and P_{max} were computed with the photosynthetic irradiance response curve according to Bassman and Zwier (1991).

P_N-C_i curve was fitted with linear equation ($P_N = k\ C_i + i$) within 50–200 $\mu mol\ mol^{-1}\ C_i$, where k was carboxylation efficiency (CE), $-i/k$ was equal to CO_2 compensation concentration (Γ^*) in the absence of mitochondria respiration (Laisk 1977), which was very low under irradiation. Maximum carboxylation rate (V_{cmax}) and dark respiration rate (R_D) were calculated according to Farquhar and Sharkey (1982) as follows:

$$V_{cmax} = k\ [C_i + K_c\ (1 + O/K_o)]^2/[\Gamma^* + K_c\ (1 + O/K_o)] \tag{3}$$
$$R_D = V_{cmax}\ (C_i - \Gamma^*)/[C_i + K_c\ (1 + O/K_c)] - (k\ C_i + i) \tag{4}$$

where K_c and K_o are Michaelis-Menten constant of ribulose-1,5-bisphosphate carboxylase/oxygenase for carboxylation and oxidation, respectively, which are temperature dependent (Niinemets and Tenhunen 1997), and O is intercellular oxygen concentration, close to 210 mmol mol^{-1}. Maximum electron transport rate was calculated according to Loustau *et al.* (1999) as

$$J_{max} = [4\ (P_{max} + R_D)(C_i + 2\Gamma^*)]/(C_i - \Gamma^*) \tag{5}$$

Several leaf discs from each sample leaf were taken using a definite area punch. Major leaf veins were avoided. Leaf discs were oven-dried at 80 °C for 48 h and weighed with an analytic balance. Leaf nitrogen was extracted in H_2SO_4 and analysed using Kjeldahl method (*BUCHI Auto Kjeldahl Unit K-370, BUCHI Labortechnik*, Schweiz). The analysis was performed in Biogeochemistry Laboratory of XTBG, the Chinese Academy of Sciences. Chl and carotenoid contents were determined following the method of Lichtenthaler and Wellburn (1983).

Photosynthetic nitrogen utilization efficiency (PNUE) was expressed as the ratio of P_{max} to N content. Nitrogen allocated to carboxylation (P_C), bioenergetics (P_B), and light-harvesting components (P_L) of photosynthetic machinery were calculated according to Niinemets and Tenhunen (1997). In this paper, these variables were represented as V_{cmax}/N_A, J_{max}/N_A, and Chl_A/N_A, which were related proportionally to P_C, P_B, and P_L, respectively. This could ensure that irradiance response patterns of N allocation would not be changed while remaining the real values of maximum carboxylation and electron transport rates per unit nitrogen. CE/N_A was also presented to show N allocation to carboxylation.

Effects of species, irradiances, and their interaction on variables measured in this study were evaluated with a two-way ANOVA. The relative importance of each independent factor on each variable was evaluated according to the function of "estimates of effect size". Post-hoc tests were done to differentiate the differences among species and among irradiances if their effects were significant. The responsive curves of variables to irradiance, LMA, and RD were fitted for each species with nonlinear models (the best equation was used for each curve). All the analyses were carried out using *SPPS 10.0* (*SPSS*, Chicago, IL, USA).

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Results

All the seedlings of *Gynura* died in a few days after being transferred to 4.5 % irradiance, while all the seedlings of *Ageratina* and *Chromolaena* survived at 4.5 % irradiance through the study. Almost all of the surviving seedlings lay prostrate on ground with slender stems and few small sized leaves. They grew very slowly and did not produce enough leaves for destructive measurement. Therefore, no LMA and N data were provided for 4.5 % irradiance.

Irradiances (except for J_{max}/N_A, and CI) and species significantly affected all the traits measured in this study (Table 1). There were no interactions between irradiance and species. Species was the main determinant of PNUE, J_{max}/N_A, and CI, while other variables were mainly determined by irradiance according to the results of estimates of effect size.

Table 1. The influence of irradiance and species on resources' capture-related variables. Results of a two-way ANOVA and post-hoc tests with irradiances ($n = 4$) and species ($n = 3$) as independent variables. One of the three F-values of each variable is given in **bold**, whose corresponding factor was the main determinant of the variable according to the results of estimates of effect size test. $^{**}p<0.01$; $^{***}p<0.001$. *Different letters* following the means indicate significant difference among species (Duncan test, $p<0.05$). LMA, leaf mass per area [g m^{-2}]; P_{max}, photon saturated photosynthetic rate per leaf area [μmol m^{-2} s^{-1}]; P_{max-M} photon-saturated photosynthetic rate per leaf mass [mmol kg^{-1} s^{-1}]; J_{max}, maximum electron transport rate [μmol m^{-2} s^{-1}]; V_{cmax}, maximum carboxylation rate [μmol m^{-2} s^{-1}]; CE, carboxylation efficiency; R_D, dark respiration rate [μmol m^{-2} s^{-1}]; N_A, leaf nitrogen content per area [g m^{-2}]); N_M, leaf nitrogen content per mass [%]; PNUE, photosynthetic nitrogen utilization efficiency [mmol kg^{-1} s^{-1}]; CI, compensation irradiance [μmol mol^{-1}].

Variable	F-values			r^2	Species means		
	Irradiance, I	Species, S	I×S		*Ageratina*	*Chromolaena*	*Gynura*
LMA	**169.07***	7.77**	0.14	0.96	22.71 b	25.34 a	22.42 b
P_{max}	**35.09*****	7.30**	0.37	0.84	15.10 b	14.35 b	17.88 a
P_{max-M}	**24.76*****	30.07***	0.01	0.87	0.67 b	0.58 b	0.81 a
J_{max}	**14.18*****	10.78***	0.62	0.74	225.46 a	213.82 a	168.39 b
V_{cmax}	**32.32*****	15.18***	0.61	0.85	95.65 a	67.52 c	80.87 b
CE	**44.77*****	14.54***	0.93	0.87	0.13 a	0.10 c	0.11 b
R_D	**16.54*****	18.16***	0.16	0.80	2.24 a	0.78 b	1.04 b
N_A	**28.35*****	16.87***	0.03	0.85	0.96 a	0.86 b	0.77 c
N_M	**14.27*****	5.99**	0.16	0.73	3.86 a	3.52 b	3.37 b
PNUE	9.77***	**26.78*****	0.28	0.79	15.40 b	16.64 b	23.00 a
J_{max}/N_A	0.68	**12.34*****	0.49	0.57	234.30 b	197.73 c	282.80 a
V_{cmax}/N_A	**9.79*****	12.41***	0.16	0.73	97.58 a	78.09 b	105.21 a
CE/N_A	**9.27*****	10.74***	0.25	0.71	0.13 b	0.12 c	0.15 a
CI	2.37	**31.13*****	0.94	0.74	37.25 a	20.02 b	18.54 b

For all the three exotics, P_{max}, J_{max}, V_{cmax}, and CE increased with irradiance (Fig. 1), LMA (Fig. 2), and R_D (Fig. 3). LMA and R_D also increased with irradiance (Figs. 2 and 3). Mass based P_{max-M} increased with irradiance, and decreased after reaching the highest value at intermediate irradiance (Fig. 1*E*). The influence of irradiance on CI was not significant (Table 1 and Fig. 1*F*). Among species, *Ageratina* showed the highest values in J_{max}, V_{cmax}, CE, and CI; *Gynura* the highest values in P_{max} and P_{max-M} (Table 1 and Fig. 1*A-E*).

Chromolaena was significantly higher in LMA than *Ageratina* and *Gynura* (Table 1 and Fig. 2). At the same LMA, *Gynura* showed the highest P_{max} although the differences among species were not significant at low LMA; *Ageratina* the highest V_{cmax} and CE; J_{max} was similar in *Gynura* and *Ageratina*; *Chromolaena* exhibited the lowest values in the four variables. *Ageratina* was significantly higher in R_D than *Gynura* and *Chromolaena* (Table 1 and Fig. 3). At the same R_D, *Ageratina* generally

showed the lowest, while *Gynura* the highest *photo-synthetic* variables.

With the increase of irradiance, N_A increased continuously for *Ageratina* and it reached the highest values at intermediate irradiance for *Chromolaena* and *Gynura* (Fig. 4*A*). For *Ageratina* and *Chromolaena*, N_M decreased, but for *Gynura* it increased to the highest value at 50 % irradiance, then decreased (Fig. 4*B*). For *Chromolaena*, PNUE increased continuously, but for *Ageratina* and *Gynura* it peaked at intermediate irradiance (Fig. 4*C*). For *Gynura* and *Chromolaena*, V_{cmax}/N_A and CE/N_A, indicators of N allocation to carboxylation component of photosynthetic apparatus, increased but for *Ageratina*, they peaked at intermediate irradiance (Fig. 4*E,F*). In contrast, Chl_A/N_A, an indicator of N allocation to light-harvesting components, decreased continuously with irradiance for *Gynura* and *Chromolaena*, but *Ageratina* reached the highest values at intermediate irradiance (data not shown). J_{max}/N_A, an indicator of N
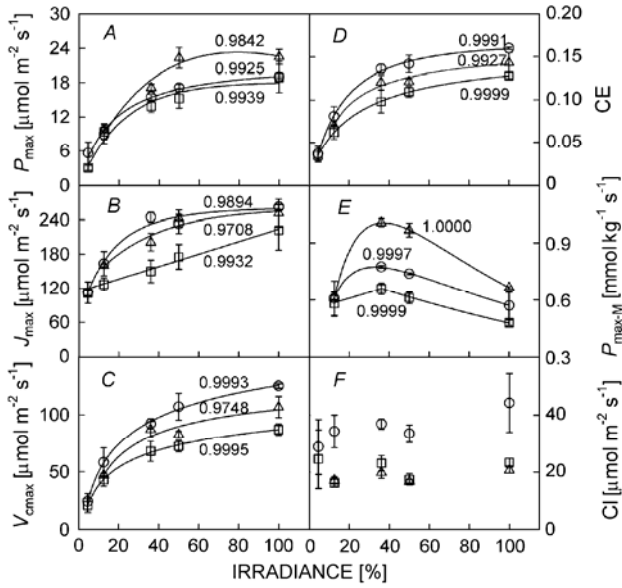
Fig. 1. Photon-saturated photosynthetic rate, P_{max} (A), maximum electron transport rate, J_{max} (B), maximum carboxylation rate, V_{cmax} (C), carboxylation efficiency, CE (D), photon-saturated photosynthetic rate per unit leaf mass, P_{max-M} (E), and compensation irradiance, CI (F) in *Ageratina* (circles), *Chromolaena* (squares), and *Gynura* (triangles) grown at different irradiances. Mean±SE (n = 5). *Numbers* in each plot are r values of the fitted curves.
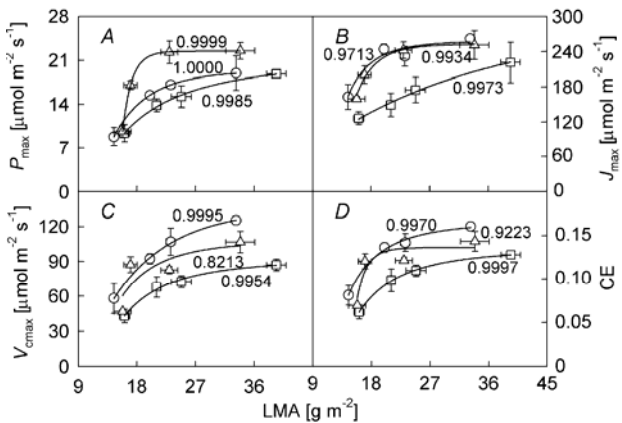

Fig. 2. Photon-saturated photosynthetic rate, P_{max} (A), maximum electron transport rate, J_{max} (B), maximum carboxylation rate, V_{cmax} (C), and carboxylation efficiency, CE (D) as a function of leaf mass per unit area (LMA) for *Ageratina* (circles), *Chromolaena* (squares), and *Gynura* (triangles) grown at different irradiances. Mean±SE (n = 5). *Numbers* in each plot are r values of the fitted curves. For each species, the symbols from left to right in each plot represent the data for seedlings grown at 12.5, 36, 50, and 100 % irradiances, respectively.

allocation to bioenergetics, was not significantly affected by irradiance (Table 1 and Fig. 4D). Among species, *Ageratina* exhibited the highest N_A and N_M, while *Gynura* the highest PNUE, J_{max}/N_A, V_{cmax}/N_A, and CE/N_A (Table 1 and Fig. 4).
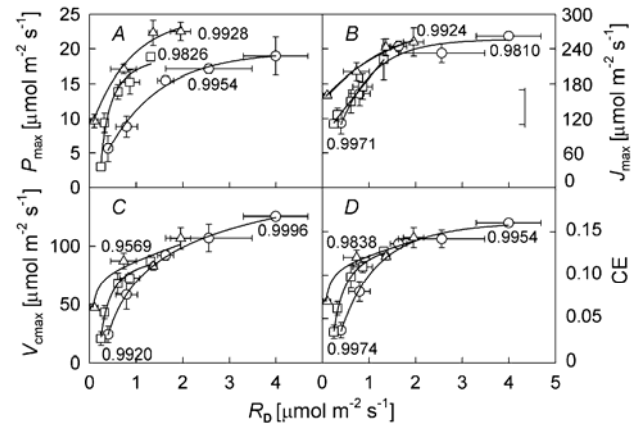

Fig. 3. Photon-saturated photosynthetic rate, P_{max} (A), maximum electron transport rate, J_{max} (B), maximum carboxylation rate, V_{cmax} (C), and carboxylation efficiency, CE (D) as a function of dark respiration rate (R_D) for *Ageratina* (circles), *Chromolaena* (squares), and *Gynura* (triangles) grown at different irradiances. Mean±SE (n = 5). *Numbers* in each plot are r values of the fitted curves. For each species, the symbols from left to right in each plot represent the data for seedlings grown at 4.5 (for invaders only), 12.5, 36, 50, and 100 % irradiances, respectively.
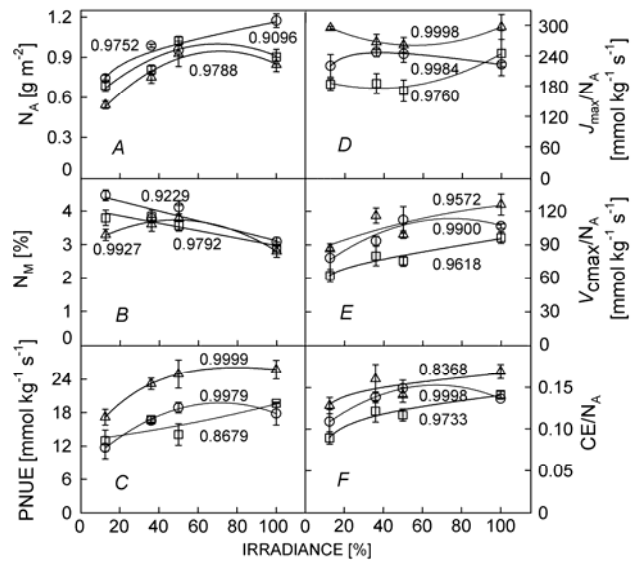

Fig. 4. Leaf nitrogen content per area, N_A (A) and per mass, N_M (B), photosynthetic nitrogen utilization efficiency, PNUE (C), and the ratios of maximum electron transport rate, J_{max} (D), maximum carboxylation rate, V_{cmax} (E), and carboxylation efficiency, CE (F) to N_A, respectively, for *Ageratina* (circles), *Chromolaena* (squares), and *Gynura* (triangles) grown at different irradiances. Mean±SE (n = 5). *Numbers* in each plot are r values of the fitted curves.

The diurnal change patterns of Φ_{PS2} (Fig. 5A–C) were opposite to those of incident PPFD (data not shown) on a clear day. With the increase of PPFD, Φ_{PS2} decreased in the morning and increased with the decrease of PPFD in the afternoon. In contrast, NPQ increased in the

morning, reached highest value at noon, and then decreased (Fig. 5*D–F*). The diurnal fluctuation magnitudes of Φ_{PS2} and NPQ for all species increased with increasing irradiance, and were less for *Gynura* at high irradiance. The diurnal fluctuations were very small for all species grown at low irradiance. The values of NPQ and Φ_{PS2} in late afternoon were similar to those in the early morning for *Ageratina* and *Gynura*, but the value of NPQ was slightly higher in late afternoon for *Chromolaena*.
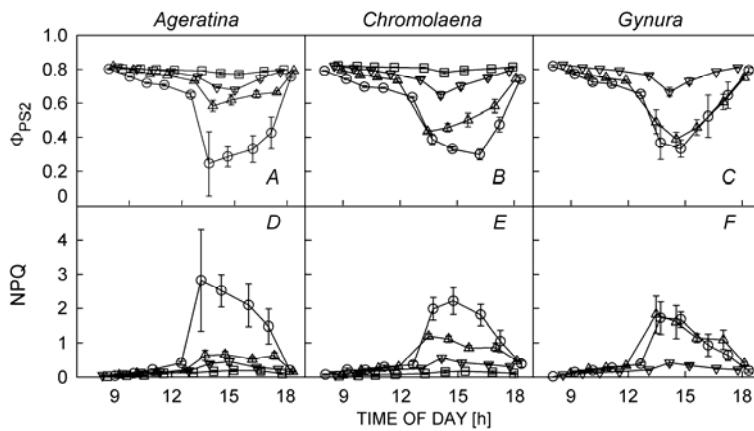

Fig. 5. Diurnal fluctuations of actual photochemical efficiency of photosystem 2, Φ_{PS2} (*A*, *B*, *C*), and non-photochemical quenching coefficient, NPQ (*D*, *E*, *F*) for *Ageratina* (*A*, *D*), *Chromolaena* (*B*, *E*), and *Gynura* (*C*, *F*) grown at 100 (*circles*), 50 (*triangles up*), 12.5 (*triangles down*), and 4.5 (*squares*) % irradiances. Mean±SE (*n* = 5). The diurnal change patterns of Φ_{PS2} and NPQ for each species grown at 36 % irradiance was similar to those for the same species grown at 50 % irradiance; they were not shown in the plots for the sake of clarity.
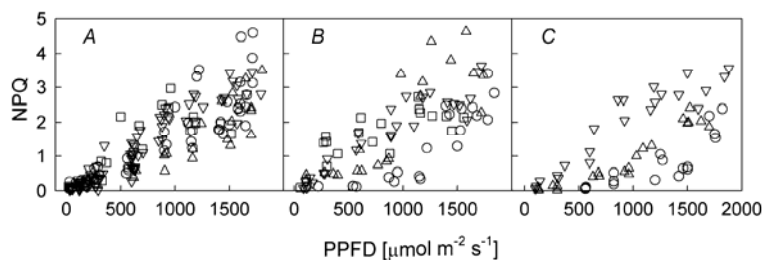

Fig. 6. Response of non-photochemical quenching coefficient, NPQ to PPFD for *Ageratina* (*A*), *Chromolaena* (*B*), and *Gynura* (*C*) grown at 100 (*circles*), 50 (*triangles up*), 12.5 (*triangles down*), and 4.5 (*squares*) % irradiances.

For the three species, NPQ increased curvi-linearly with "actinic light", especially for seedlings grown at high irradiance (Fig. 6). *Ageratina* and *Chromolaena*, grown at 4.5 and 12.5 % irradiances, exhibited higher NPQ within low PPFD range (roughly <1 000 µmol m^{-2} s^{-1}) but lower NPQ within higher PPFD range than those grown at 40 and 100 % irradiances. However, *Gynura* showed higher NPQ at 12.5 % irradiance than at higher irradiances. The two invaders grown at high irradiance had higher thermal dissipation ability according to NPQ than those grown at low irradiance.

Discussion

As expected, the two invaders, *Ageratina* and *Chromolaena*, could acclimate to a wider range of irradiances than the NIN alien, *Gynura*. They could survive, grow, and keep relatively high photosynthetic and thermal dissipation ability at 4.5 % irradiance (Figs. 1 and 6), which was uncommon for light-demanding species. The high photosynthetic and thermal dissipation potential would benefit the invaders when high irradiance was abruptly encountered after, for example, disturbance. But surprisingly the two invaders did not show distinctly lower LMA (Table 1) and lower leaf-level CI (Fig. 1*F*). Biomass allocation-related traits might be associated with the differences in shade tolerance between the IN and NIN aliens (Feng *et al.* 2007). The high shade tolerance ability might be correlated with the two invaders' invasiveness. Having high shade tolerance ability and still maintaining large growth rates at high irradiance is related to invasiveness of exotic species (Niinemets *et al.* 2003).

Surprisingly, the two invaders did not exhibit higher resource capture ability and efficiency. Although having

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higher biochemical capacity for photosynthesis, *i.e.* higher J_{max}, V_{cmax}, and CE (Fig. 1*B–D*), *Ageratina* showed lower P_{max} than *Gynura* due at least partially to its higher R_D. The three aliens showed curvilinear relationships between R_D and P_{max}, J_{max}, V_{cmax} as well as CE. At the same R_D, the invaders showed lower both biochemical and photosynthetic capacity (Fig. 3). The invaders did not reduce carbon costs of resources gain. This is different from the results of Pattison *et al.* (1998) and McDowell (2002). They reported that P_{max} increases with R_D linearly and invasive species exhibit higher P_{max} than native species.

Another designator of carbon costs of resources' gain is LMA which is associated with plant functions such as carbon assimilation and carbon allocation (Reich *et al.* 1997, Feng *et al.* 2004, Zhang and Feng 2004). Generally, species with higher growth rate have lower LMA (Reich *et al.* 1997). The great success of IN species is partially attributed to their thinner leaves, and therefore lower carbon cost per unit photosynthetic area (Baruch and Goldstein 1999, Durand and Goldstein 2001). We assumed that P_{max}/LMA was a more important indicator of the carbon costs of resources' gain than LMA. It is not always profitable for species to decrease LMA with concomitant equal or greater decrease of P_{max}. Decreasing LMA meanwhile maintaining equal or even higher P_{max} is beneficial for species, especially at high irradiance. However, the two invaders did not show consistent lower LMA than *Gynura*, which was consistent with the result of Smith and Knapp (2001). McDowell (2002) found that IN species exhibit higher LMA than native species. Furthermore, at the same LMA, photosynthetic carbon gain was also lower for the two invaders although *Ageratina* showed higher V_{cmax} and CE (Fig. 2*C,D*).

In addition, the two invaders did not show higher PNUE than *Gynura* (Fig. 4*C*) as expected. Compared with the two invaders, *Gynura* showed lower N content and higher PNUE (Table 1, Fig. 4*A–C*). McDowell (2002) found that IN species exhibit lower N_M but higher PNUE. However, both the studies are consistent with the conclusion that PNUE is inversely related to N content (Chapin 1991). However, Baruch and Goldstein (1999) and Durand and Goldstein (2001) found that IN species have higher both N content and utilization efficiency than native species. As a group, the three aliens showed higher N_M and PNUE (Fig. 4*B,C*) than other exotic species (Baruch and Goldstein 1999, Durand and Goldstein 2001, McDowell 2002, Ewe and Sternberg 2003, Niinemets *et al.* 2003) and tropical native herbaceous species (Reich and Oleksyn 2004), leading to higher P_{max}.

The increase of P_{max} with irradiance is mainly attributed to the increase of LMA (Niinemets and Tenhunen 1997, Rosati *et al.* 1999, Le Roux *et al.* 2001). Indeed, our results indicated that LMA was an important factor explaining the increase of P_{max}, J_{max}, V_{cmax}, and CE with irradiance, but it was not the only or even not the main reason for the increased P_{max} (Fig. 2). In low irradiances,

the increment of P_{max-M} was much bigger than that of P_{max} (Fig. 1*A,E*), indicating that other factors contributed to the increased P_{max}.

The increased N_A (Fig. 4*A*) might contribute to the increased P_{max} for the three aliens because N content is positively related to photosynthesis (Le Roux *et al.* 2001, Vincent 2001, Walcroft *et al.* 2002, Zhang and Feng 2004). However, the increased LMA might also affect the changes in N_A as N_M decreased with irradiance (Fig. 4*B*), suggesting that the contribution of the increased N_A to P_{max} was also related to morphological trait. The increased PNUE (Fig. 4*C*) might be another factor contributing to the increased P_{max} because PNUE is one of the main factors determining photosynthetic capacity (Rosati *et al.* 1999, Vincent 2001).

The differences in N allocation among different components of photosynthetic apparatus are associated with the increase of PNUE with irradiance (Niinemets and Tenhunen 1997, Rosati *et al.* 1999, Le Roux *et al.* 2001, Walcroft *et al.* 2002, Zhang and Feng 2004). At high irradiance, the aliens increased N allocation to carboxylation but decreased those to light-harvesting components as represented by V_{cmax}/N_A, CE/N_A (Fig. 4*E,F*), and Chl_A/N_A, promoting PNUE and P_{max}, and reducing photon capture and excessive photon energy. No distinct increase of N allocation to bioenergetics was detected according to J_{max}/N_A at high irradiance (Fig. 4*D*).

The three aliens grown at high irradiance had high P_{max} (Fig. 1*A*), which was consistent with other light-demanding species (Kitao *et al.* 2000, Warren and Adams 2001, Feng *et al.* 2004). Utilizing more photon energy through photosynthesis could help avoid possible damages caused by excessive photon energy and protect photosynthetic machinery from photodamage (Scholes *et al.* 1997, Kitao *et al.* 2000, Feng *et al.* 2002b). Thermal dissipation, which can be estimated by NPQ value, can also reduce excessive energy and alleviate photodamage (Feng *et al.* 2002a). Within low PPFD range (<1 000 µmol m^{-2} s^{-1}), NPQ was lower and increased with PPFD more slowly for the aliens grown at high irradiances with high P_{max} than for the aliens grown at lower irradiances with lower P_{max} (Figs. 1*A* and 6). Within higher PPFD range, thermal dissipation increased sharply with PPFD for the three aliens grown at high irradiances because the increase of photosynthesis with PPFD was reduced in high PPFD, leaving more excessive energy. In a clear day the diurnal maximum NPQ values (Fig. 5*D–F*) for each species were much lower than the maximum values in PPFD response curves (Fig. 6) for the same species, indicating that the aliens did not fully operate their thermal dissipation ability. The results indicated that the three aliens protected photosynthetic apparatus from photodamage mainly through photosynthetic use of photon energy, which might be a common attribute of light-demanding species (Scholes *et al.* 1997, Kitao *et al.* 2000, Feng *et al.* 2002b).

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