Response of invasive *Chromolaena odorata* and two coexisting weeds to contrasting irradiance and nitrogen

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Abstract

Chromolaena odorata is a widespread exotic weed in southern China and other regions of the world. To better understand its invasive strategies, we compared leaf pigment contents and gas-exchange traits of the invader with its two coexisting species (native *Urena lobata* and invasive *Bidens pilosa*) under combined conditions of irradiance (full, medium, and low) and nitrogen (full, medium, and low) supplies. The chlorophyll (Chl) *a*+*b* content of *U. lobata* was the highest and the Chl *a*/*b* ratio of *C. odorata* was the lowest among the three weed species. In most treatments, leaf pigment, light-saturated photosynthetic rate (P_{max}), and light saturation point (LSP) of all the species increased, while their Chl *a*/*b* ratios decreased with the increasing nitrogen. The P_{max} and LSP of *U. lobata* were greater than those of the coexisting weeds under full irradiance (FI), but significantly declined with the decreasing irradiance. The invasive weeds, especially *C. odorata,* showed lower P_{max} and LSP under FI, but they showed slight decrease under low irradiance. Compared to *U. lobata, C. odorata* exhibited the lower light compensation point (LCP) in most treatments, higher LSP under low and medium irradiance, and lower dark respiration rate under FI. In addition, all the three species showed similar responses to different irradiance and nitrogen conditions, mean phenotypic plasticity index (MPPI) of most photosynthetic variables of the two invasive species was lower than that of *U. lobata.* These results suggested that *C. odorata* behaved as a facultative shade-tolerant weed, being able to grow in moderately sheltered environments; the lower MPPI might be one of the important competitive strategies during its invasion. However, its invasion should be limited to some very shady habitats. In the field, control should be mainly directed against populations growing in the open or nutrient-rich habitats, where its expansion speed could be much faster. Deep shade by intact canopies or luxuriant forests might be an effective barrier against its invasion.

Additional key words: gas exchange; invasive species; irradiance; nitrogen supply; pigment.

Introduction

Exotic plant invasion is a serious environmental problem and a threat to natural ecosystems worldwide. Invasive plants often grow aggressively and displace native plants by forming dense monocultures, causing great damage to native ecosystems (D'Antonio and Kark 2002). For example, invasive plants reduce plant species richness and biodiversity (Brewer 2008, Davies 2011), alter soil property and nutrient cycling process (Rodgers *et al.* 2008, Strickland *et al.* 2011, Chau *et al.* 2013), and affect ecosystem structure and function (Gaertner *et al.* 2011, Sousa *et al.* 2011). Identifying the factors that contribute to the success of exotic plant invasions is very important, not only for understanding the invasive mechanisms of exotic plants but also for predicting and controlling the spread of invasive species.

Many scientific studies showed that leaf physiological traits of invasive species, such as photosynthetic rate and water-use efficiency, were higher than those of native

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Abbreviations: BP – *Bidens pilosa*; Chl – chlorophyll; CO – *Chromolaena odorata*; FI – full irradiance; g_s – stomatal conductance; HN – high nitrogen content; LCP – light compensation point; LI – low irradiance; LN – low nitrogen content; LSP – light saturation point; MI – medium irradiance; MN – medium nitrogen content; MPPI – mean phenotypic plasticity index; P_{max} – light-saturated photosynthetic rate; P_N – net photosynthetic rate; R_D – dark respiration rate; SLA – specific leaf area; UL – *Urena lobata*; WUE_i – intrinsic water-use efficiency.

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or noninvasive species (Pattison *et al.* 1998, Xu *et al.* 2007, Mcalpine *et al.* 2008, van Kleunen *et al.* 2010). Photosynthetic traits related to carbon gain can directly influence plant fitness, and thus differences between invasive and native species may reflect an invader's strategy of competition (Mcalpine *et al.* 2008). For example, invasive plants with high photosynthetic capacity generally exhibit high rates of growth, biomass accumulation and overall production, and therefore they may be able to outcompete slower growing species and contribute to invasion success (Feng *et al.* 2007a, van Kleunen *et al.* 2010). However, physiological traits of plants are usually influenced by varying ambient conditions, especially limited by unfavourable environments. Irradiance and nitrogen are the core resources regulating the survival, growth, and distribution of plants (Feng *et al.* 2007a, Qing *et al.* 2011). The ability of plants to utilize these two resources is a significant determinant of growth potential and fitness (Feng *et al.* 2009).

Chromolaena odorata (L.) R. M. King & H. Robinson is a long-lived, perennial herbaceous shrub of Compositae family native to Mexico, the West Indies, and tropical America and has become a worldwide invasive species (McFadyen *et al.* 1996). In China, *C. odorata* was first discovered in Yunnan and Hainan provinces in 1934; now it is rapidly expanding throughout the southern China and became the serious threats to biodiversity, agricultural production, and ecological security. Most researches have suggested that the possible invasive mechanisms of *C. odorata* may include propagule supply, allelopathy, ecological adaptability, and phenotypic plasticity (Honu and Dang 2002, Feng *et al.* 2007b, Sangakkara *et al.* 2008, Zhang *et al.* 2009). Several studies showed that *C. odorata* is a light-favoring species with much greater seed production and stronger allelopathy effect (Witkowski and Wilson 2001, Feng *et al.* 2007a). Others reported that *C. odorata* exhibits higher ecological adaptability to temperature and soil water, and high nutrient concentrations significantly increased its invasive competitiveness (Lu *et al.* 2008, Zhang and Wen 2009, Qin *et al.* 2013). Additionally, *C. odorata* could accumulate soil pathogens to inhibit native plants in its invaded ranges (Mangla *et al.* 2008). These traits help *C. odorata* to gain more competitive advantages during its invasion process in the fields. A knowledge of how *C. odorata* responds to irradiance and nitrogen interactions with respect to its leaf physiological traits is important for understanding its ecophysiological acclimation and invasive strategy, which has not been yet adequately understood. We investigated the effect of various irradiances and nitrogen supplies on leaf pigment, photosynthetic capacity, and MPPI of *C. odorata* and compared it to two coexisting species. MPPI reflects the degree of phenotypic plasticity for an organism acclimated to heterogeneous environments (Valladares *et al*. 2000). In general, species with high plasticity have higher adaptability, which enables them to grow and reproduce in a more extensive environment (Brock *et al.* 2005, Richards *et al*. 2006, Hulme 2008). We hypothesized that compared to the two coexisting plants, *C. odorata* would have higher photosynthetic capacity under the high irradiance and in nutrient-rich environments, but lower photosynthetic capacity under the low irradiance and in nutrient-poor environments, and it would show greater phenotypic plasticity of physiological parameters in response to irradiance or nitrogen. The main objectives of this study were to determine: (*1*) how three species acclimate to different irradiance and nitrogen conditions in terms of leaf pigment and gas-exchange traits; (*2*) whether *C. odorata* exhibits higher phenotypic plasticity of leaf physiological traits than the two coexisting species.

Materials and methods

Study site and plants: The study was carried out in the greenhouse of College of Agriculture, South China Agricultural University, which is located in Guangzhou (23°16′N, 113°35′E), Guangdong Province, China. The mean annual temperature is 22.3°C in this area. The mean temperature in July, the hottest month, is 27.9°C, and 13.5°C in January, the coolest month. The average annual precipitation is 2,145 mm. During the experimental period, the midday mean photosynthetically active radiation varied between 1,300 and 1,600 μmol m^{-2} s^{-1}, and the air relative humidity varied between 60% and 75%. In this study, *C. odorata* and its two coexisting perennial forbs were investigated. *Urena lobata* L., is a perennial subshrub-like herb of Malvaceae family, native to China, Thailand, Vietnam, Cambodia, and southeast Asia. It is a very common plant which spread widely in most areas of southern China and can be outcompeted by *C. odorata* in the field. *Bidens pilosa* L. is another perennial herb or shrub of Compositae family, native to Central and South America, which has invaded much of the tropics and subtropics in the world, especially in Asia. It was first discovered in Hongkong in 1857, and now it has infested in almost all the provinces of central and southern China, such as Guangdong, Hainan, Yunnan, Hubei, Jiangsu, Zhejiang, *etc*. It has damaged biodiversity and the structure and function of invaded ecosystems. But the degree of its invasiveness is lower than that of *C. odorata* according to field observations in the study area. The two forbs are 0.5–1.5 m tall and co-occur with *C. odorata* in most habitats, including croplands, plantations, wastelands, pastures, disturbed forests, roadsides, riverbanks, *etc*.

Seeds of *U. lobata* and *B. pilosa* were collected from eight and ten maternal plants of the same populations at Zengcheng Teaching and Research Farm of South China Agricultural University in December 2009 and June 2010, respectively. Those of *C. odorata* were collected from five maternal plants of the same populations in Danzhou city (19°31′N, 109°34′E), Hainan Province, China, in April 2010. The three weed populations, which we collected seeds from, were grown in the wasteland with sufficient sunshine and medium nutrient supply. To obtain similarly sized seedlings, fully developed and midsized seeds of *C. odorata* and *U. lobata* were sown separately in two seedbeds under 75% irradiance on 26 July 2010, and those of *B. pilosa* were sown on 2 August 2010. Because of a poor germination rate and lack of seedlings, we collected current-year seedlings of *U. lobata* (with 2–3 leaves and about 4 cm high) from the field and planted them in a seedbed on 10 August 2010. After four weeks (10 September 2010), the seedlings of the three species were transplanted singly into plastic pots (upper diameter of 20 cm, basal diameter of 16 cm, height of 19 cm), and each pot was filled with river sand (3 kg per pot) and placed with a salver on its bottom. All the seedlings were grown under 75% irradiance.

Irradiance and nitrogen treatments: Irradiance levels used in this study were reached by covering the shade sheds with different layers of black nylon shade netting, including no netting to enable 100% irradiance (full irradiance, 100% radiation inside the greenhouse, about 1,300-1,600 μmol(photon) m^{-2} s^{-1} at midday). The relative irradiance in each shade shed was estimated by comparing the integrated PPFD during a clear day with that in a shade shed with no netting. Three shade sheds (each is 7.0 m length × 4.0 m width × 2.5 m height) were constructed in the same greenhouse in August 2010. The lower 30 cm of each shade shed remained open to facilitate airflow and to maintain humidity and temperature levels as similar as possible between the shade sheds.

On 17 September 2010, 108 vigorous seedlings of about 20 cm high for each species were subjected to the combined irradiance and nitrogen treatments:

Irradiance treatment		
Full	FI	no shade netting (100% of available radiation)
Medium	MI	one layer of black nylon shade netting (42–45% of available radiation)
Low	LI	two layers of black nylon shade netting (15–18% of available radiation)

Nitrogen concentration			Added per pot during the experiment
High	HN	0.6 g(N) kg^{-1}(sand)	1.80 g carbamide (with 46% available nitrogen)
Medium	MN	0.3 g(N) kg^{-1}(sand)	0.90 g carbamide
Low	LN	0.06 g(N) kg^{-1}(sand)	0.18 g carbamide

Distance of each shed was approximately 3 m to prevent from shading. Three nitrogen concentrations were applied for each irradiance treatment:

Nitrogen was applied on 17 September and 30 October, respectively, with half of total carbamide at each time. There were in total 27 treatments (3 species × 3 irradiance × 3 nitrogen concentrations), and for each treatment 12 replicates were used in this study. At four-day intervals, Hoagland nutrient solution with no nitrogen was added to each pot to ensure the rest of nutrition supplies for plant growth. The seedlings were watered with tap water every day during the experiment.

Measurements: Before harvest, the leaf Chl content was analyzed using the method described by Dere *et al*. (1998), and the extracting solvent was 100% acetone.

Leaf gas exchange was determined using a *Li-6400* portable photosynthesis system (*LiCor Inc.*, Lincoln, NE, USA) in the middle of November 2010. On each sampling day, five to eight plant individuals per species and per treatment were selected and one fully developed, unshaded representative leaf per plant was measured. Conditions in the leaf chamber were controlled automatically, with leaf temperature of 25°C and airflow of 0.5 L min^{-1}. PPFD was supplied at 2,000; 1,500; 1,000; 800, 600, 400, 200, 150, 100, 80, 50, 20, and 0 μmol(photon) m^{-2} s^{-1}, decreasing in a stepwise fashion. Data were recorded when the leaf was illuminated for 3 min under each irradiance step. The measurements were taken between 8:30 and 11:30 h. P_{max} was calculated by the exponential equation of Bassman and Zwier (1991):

$$P_N = P_{max}\,(1 - Co\ e^{-a\,PPFD/P_{max}})$$

where P_N is the net photosynthetic rate [μmol(CO_2) m^{-2} s^{-1}], P_{max} is the light-saturated photosynthetic rate [μmol(CO_2) m^{-2} s^{-1}], a is the quantum yield under low PPFD and *Co* is the dimensionless coefficient when P_N approaches zero under low PPFD. LCP is calculated when P_N approached zero, and LSP is calculated when P_N reached 99% of P_{max}. Parameters of the model were calculated by the nonlinear estimation module of *SPSS 13.0* for *Windows* (*SPSS Inc.*, Chicago, IL, USA):

$$LCP = P_{max} \times \ln(Co)/a$$
$$LSP = P_{max} \times \ln(100\ Co)/a$$

R_D [μmol(CO_2) m^{-2} s^{-1}] is derived form linear regression of the first seven points [0–200 μmol(photon) m^{-2} s^{-1}] of each replicate curve (Allred *et al.* 2010).

In late November 2010, under fixed 1,300 μmol m^{-2} s^{-1} PPFD, we measured P_N and stomata conductance (g_s [mmol(H_2O) m^{-2} s^{-1}]) of three species in all the treatments. The intrinsic water-use efficiency (WUE_i, [μmol(CO_2) $mmol^{-1}$(H_2O)] was calculated as the ratio between P_N and g_s (Moutinho-Pereira *et al.* 2004).

MPPI is calculated according to the formulas by Valladares *et al.* (2000):

$$MPPI = 1 - x/X$$

where x and X are the minimum mean and the maximum mean values among the three irradiance/nitrogen treatments, respectively.

Statistical analyses: The effects of species, irradiance, and nitrogen on each variable evaluated in this study were tested by three-way analysis of variances (*ANOVA*) (species, irradiance, and nitrogen as source factors) with Type III sums of squares. The differences among the three species at the same nitrogen of each irradiance, the differences among the three nitrogen concentrations for the same species of each irradiance, and the differences among the three irradiances for the same species of each nitrogen were analyzed with one-way *ANOVA* (*Duncan*'s test, $p<0.05$). If necessary, data were log-transformed before *ANOVA*. All statistical analyses were conducted with *SPSS 13.0* for *Windows*. The figures were made with *SigmaPlot 12.0* (*Systat Inc.*, San Jose, CA, USA).

Results

General effects of species, irradiance and nitrogen: Species, irradiance, nitrogen, and irradiance *vs*. nitrogen showed extremely significant impacts on all variables measured in this study according to a three-way *ANOVA*; most variables showed the stronger irradiance effect (Table 1). Combination of species × irradiance exhibited the same effect on all parameters except WUE_i. The interactions among species, irradiance, and nitrogen were also significant or extremely significant for all variables, whereas Chl *a*/*b*, LSP, R_D, and WUE_i were unaffected by the species and nitrogen interactions.

Differences in leaf pigment among species: Chl (*a*+*b*) content of *U. lobata* was significantly higher than that of the two invasive weeds under all irradiances and in most treatments, whereas the Chl (*a*+*b*) content of *C. odorata* was also significantly higher than that of *B. pilosa* (Fig. 1*A*–*C*). In addition, the Chl (*a*+*b*) content of the two invasive weeds significantly increased with the decrease of irradiance. The Chl *a* and *b* contents showed a similar changing as that of Chl (*a*+*b*) in all species, but the Chl *b* content of *C. odorata* was significantly higher under MN and HN at LI than that of *U. lobata* (Fig. 1*D*–*I*). The Chl *a*/*b* ratio of *C. odorata* was the lowest and significantly lower than that of other two species in most treatments and decreased significantly with nitrogen increasing or irradiance decreasing (Fig. 1*J*–*L*).

Differences in gas-exchange traits among species: Photosynthetic rates of all species increased significantly with nitrogen increasing at FI, where *U. lobata* was the highest and *C. odorata* was the lowest under both MN and HN treatments (Fig. 2*A*–*C*). Shading led to a serious decline of the photosynthetic rate in all three weeds. Their light-response curves overlapped nearly at LI–LN, but at LI–HN, the photosynthetic rates of the two invaders were higher than that of *U. lobata* (Fig. 2*D*–*I*).

P_{max} of *C. odorata* was the lowest at FI and that of the two invasive species was significantly higher at HN under LI (Fig. 3*A*–*C*). LSP of *C. odorata* was the lowest at MN and HN under FI, while that of *U. lobata* was the lowest at MI and LI (Fig. 3*D*–*F*). P_{max} and LSP of all the species increased significantly with nitrogen increasing except for *U. lobata* at LI, and decreased notably with irradiance decreasing. But negative effects of decreasing irradiance on P_{max} and LSP of *U. lobata* were the greatest and that of *C. odorata* were the smallest.

Table 1. Results of the three-way *ANOVA* for physiological traits of the three weeds, according to the factors of species, irradiance, and nitrogen treatments. Chl − chlorophyll; P_{max} – light-saturated photosynthetic rate; LSP – light saturation point; LCP – light compensation point; R_D – dark respiration rate; g_s – stomatal conductance; WUE_i – intrinsic water-use efficiency. S − species; I − irradiance; N − nitrogen. * − $p<0.05$,** − $p<0.01$,*** − $p<0.001$. F − values; P − levels of significance (*p*); R^2 − the proportion of total variance absorbed by the model. .

Parameter	S		I		N		S×I		S×N		I×N		S×I×N		R^2
	F	P	F	P	F	P	F	P	F	P	F	P	F	P	
Chl (*a*+*b*)	1,535.85	***	1,309.59	***	562.80	***	105.81	***	22.55	***	94.24	***	19.63	***	0.99
Chl *a*/*b*	125.17	***	512.09	***	48.29	***	31.79	***	1.9		9.68	***	17.37	***	0.97
P_{max}	12.61	***	423.22	***	88.27	***	21.84	***	3.95	**	24.87	***	4.09	***	0.94
LSP	10.62	***	545.74	***	83.08	***	13.30	***	2.21		20.82	***	5.76	***	0.95
LCP	15.25	***	167.68	***	18.78	***	5.26	***	3.25	**	28.83	***	2.16	*	0.89
R_D	21.41	***	174.67	***	18.99	***	12.86	***	0.99		10.46	***	1.91	*	0.88
g_s	61.86	***	252.84	***	38.34	***	17.07	***	10.42	***	11.21	***	6.79	***	0.91
WUE_i	16.89	***	133.74	***	25.43	***	2.34		0.65		8.68	***	2.61	*	0.79

LCP of *C. odorata* was the lowest under FI and MI and that of *B. pilosa* and *U. lobata* was the highest at LI–LN and LI–HN treatment, respectively (Fig. 3 *G*–*I*). R_D of *B. pilosa* was the highest from FI to MI except for MI–MN, while the difference between *C. odorata* and *U. lobata* was not significant except for FI–HN and LI–HN, with R_D of *C. odorata* significantly lower than that of *U. lobata* (Fig. 3*J*–*L*).

The g_s of *C. odorata* was the lowest and significantly lower than that of *U. lobata* under FI and MI except for FI–LN, but the differences among all the species were not significant at LI (Fig. 3*M*–*O*). It decreased significantly with decreasing irradiance, which might lead to a high reduction in photosynthetic capacity of plants in the shade. The WUE_i of *U. lobata* was the lowest and significantly lower than that of *C. odorata* at FI and MI except for FI–LN treatment, while the difference among all the three species was not significant from MN to HN at LI (Fig. 3*P*–*R*). In addition, the WUE_i of *C. odorata* increased significantly with the increase of nitrogen under all irradiances, whereas that of *U. lobata* showed the opposite trend at FI.

Response to variation in irradiance and nitrogen: The MPPI of all three species in response to nitrogen was shown in Table 2. The MPPI for the Chl (*a*+*b*) content of two invasive weeds was higher, while the MPPI for LSP, LCP, R_D, g_s, and WUE_i was lower than that of *U. lobata*.

Meanwhile, the MPPI of all physiological parameters of two invasive weeds in response to nitrogen was 0.32 and 0.34, respectively, which was lower than that of *U. lobata* (0.40). Compared to the response to nitrogen, the response of all the species to irradiance was generally higher, with the plasticity of $P_{\max}$, LSP, R_D, and g_s higher than 50% (Table 3). The MPPI of *C. odorata* in response to irradiance was the lowest (0.56) among the three species.

Discussion

Leaf pigments: In all treatments, the Chl (*a*+*b*) content of *U. lobata* was higher than that of two invasive weeds, which would help maintain a high photosynthetic rate. It was also found that *U. lobata* had higher photosynthetic rate at FI but not at MI and LI; it suggested that other factors limiting photosynthetic capacity than the Chl (*a*+*b*) content (Fig. 2*A*–*C*) occurred (Björkman 1981). Nitrogen application or shading could increase the Chl (*a*+*b*) content of all the species; although Chl rose significantly with nitrogen at LI in the two invaders,

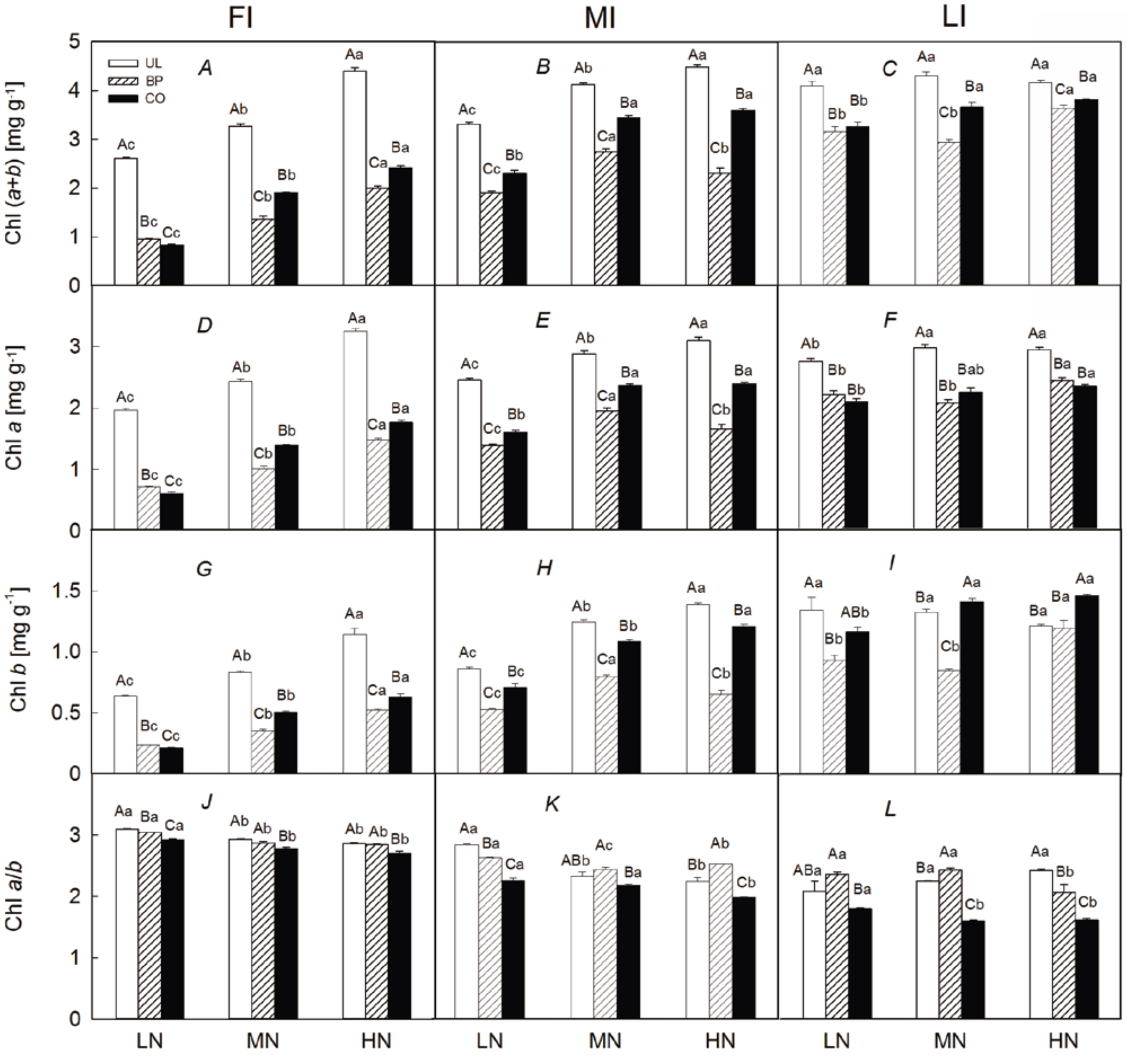

Fig. 1. Content of leaf pigment of *Chromolaena odorata*, *Bidens pilosa,* and *Urena lobata* under different irradiance and nitrogen treatments. *A, B, C*: Chlorophyll (Chl) (*a*+*b*); *D, E, F*: Chl *a*; *G, H, I*: Chl *b*; *J, K, L*: Chl *a*/*b* ratio. FI – full irradiance; MI medium irradiance; LI – low irradiance. UL – *Urena lobata* (*open bars*); BP – *Bidens pilosa* (*hatched bars*); CO – *Chromolaena odorata* (*black bars*). In each irradiance condition, seedlings of three weeds were planted under three different nitrogen concentrations. LN – low nitrogen; MN – medium nitrogen; HN – high nitrogen. Vertical bars represent SE of the mean (*n* = 4). Different *uppercase letters* indicate significant differences among species at the same irradiance and nitrogen conditions, while different *lowercase letters* indicate significant difference among nitrogen at the same irradiance condition of the same species according to *Duncan*'s test at $p<0.05$.

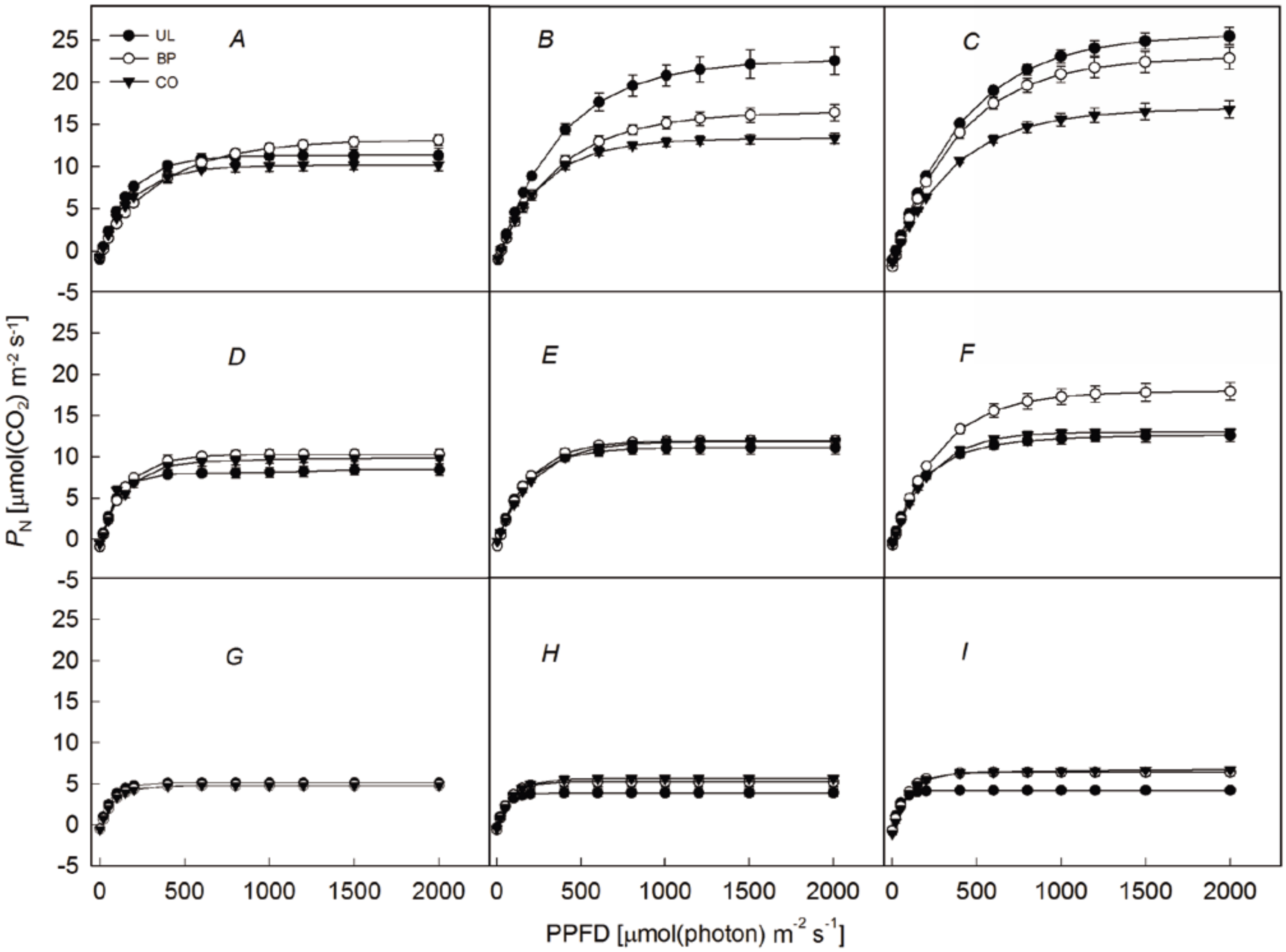

Fig. 2. Light-response curves of *Chromolaena odorata*, *Bidens pilosa*, and *Urena lobata* under different irradiance and nitrogen treatments. *A*: FI–LN, full irradiance and low nitrogen treatment; *B*: FI–MN, full irradiance and medium nitrogen treatment; *C*: FI–HN, full irradiance and high nitrogen treatment; *D*: MI–LN, medium irradiance and low nitrogen treatment; *E*: MI–MN, medium irradiance and medium nitrogen treatment; *F*: MI–HN, medium irradiance and high nitrogen treatment; *G*: LI–LN, low irradiance and low nitrogen treatment; *H*: LI–MN, low irradiance and medium nitrogen treatment; *I*: LI–HN, low irradiance and high nitrogen treatment. P_N – net photosynthetic rate; UL – *Urena lobata* (*closed circles*); BP – *Bidens pilosa* (*open circles*); CO – *Chromolaena odorata* (*closed triangles*). Vertical bars represent SE of the mean (*n* = 5–8).

U. lobata did not show any change. This might be caused by the significant increase in the Chl *b* content of two invasive weeds with rising nitrogen at LI, which was not observed in *U. lobata* (Fig. 1*I*).

The Chl *a*/*b* ratio represents shading adaptability of leaves. In general, plants with the low Chl *a*/*b* ratio exhibit higher shade tolerance (Lei *et al.* 1996). In all treatments, the Chl *a*/*b* ratios of *C. odorata* were significantly lower than those of other two species, which indicated that the Chl *b* content increased and plants were better acclimated to low irradiance. Nitrogen application or shading reduce the Chl *a*/*b* ratio of all species, which was consistent with the findings of Wang *et al.* (2003). The decrease of the Chl *a*/*b* ratio in *C. odorata* under shaded environment was the greatest because the increase of Chl *b* content was considerably higher than the Chl *a* content. A rapid decline of the Chl *a*/*b* ratio or a substantial increase of the Chl *b* content would enhance the LHCII number of *C. odorata* and its irradiance capture ability under low-light conditions, therefore plants could avoid sharp reduction in photosynthesis in the shade (Anderson and Aro 1994).

Gas-exchange traits: Photosynthetic characteristics of alien plants are closely related to their invasiveness. Many studies illustrated that invasive species usually have the higher photosynthetic capacity than native or noninvasive species (Baruch and Goldstein 1999, McDowell 2002, Mcalpine *et al.* 2008, Jiang *et al.* 2009, Wu *et al.* 2009, Zheng *et al.* 2012). High photosynthetic capability allows invasive species to accumulate more carbon and allocate it to growth and proliferation, which constitutes a solid material base to gain an advantage over native species in the competition. P_{max} is an important index of photosynthetic capacity of plants; the higher P_{max} indicates a stronger photosynthetic capacity, which is more beneficial to carbon accumulation and gain competitive advantage

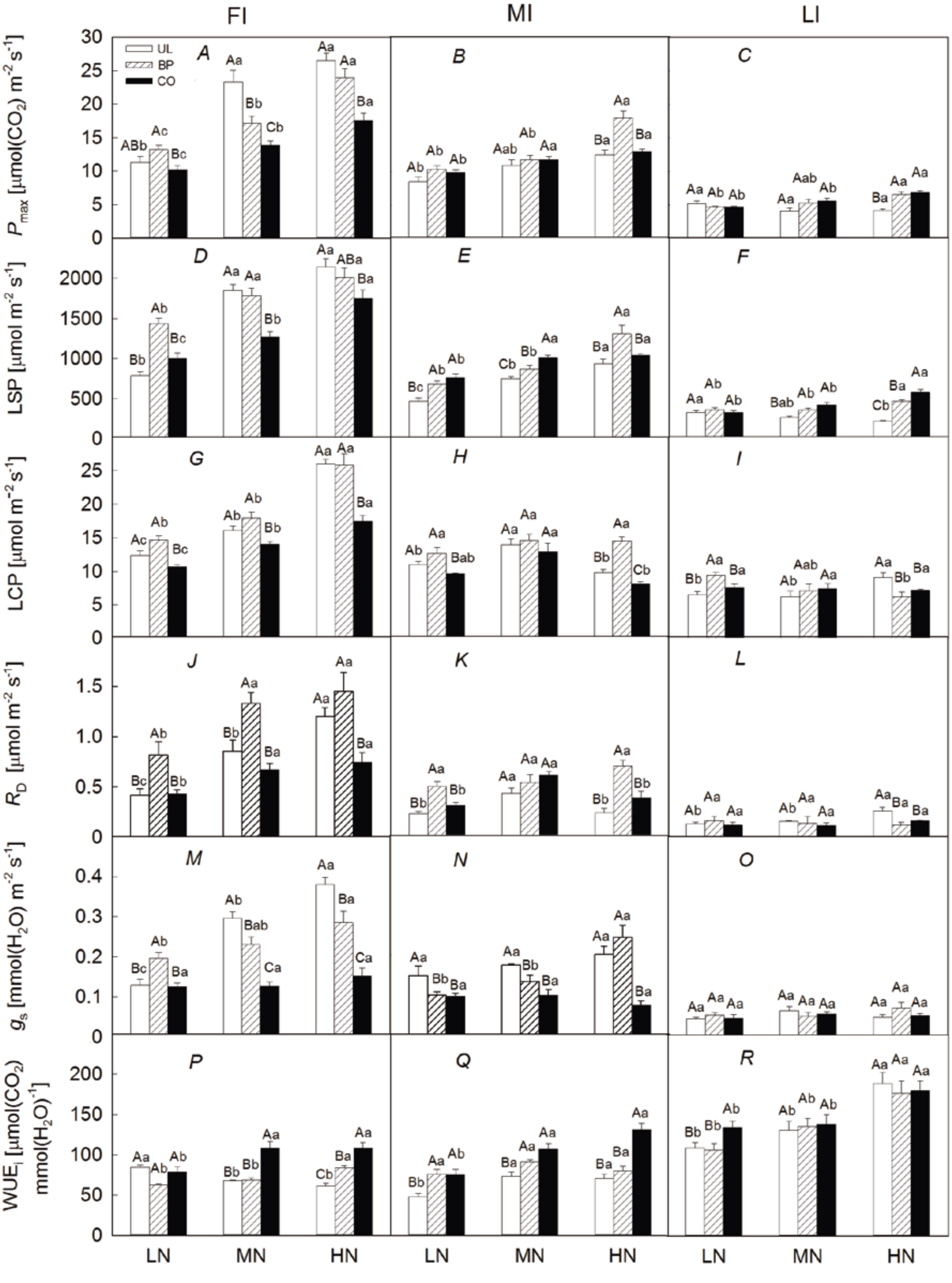

Fig. 3. General variation in gas-exchange traits of *Chromolaena odorata*, *Bidens pilosa*, and *Urena lobata* under different irradiance and nitrogen treatments. *A, B, C*: light-saturated photosynthetic rate (P_{max}). *D, E, F*: light saturation point (LSP). *G, H, I*: light compensation point (LCP). *J, K, L*: dark respiration rate (R_D). *M, N, O*: stomatal conductance (g_s). *P, Q, R*: intrinsic water-use efficiency (WUE$_i$). FI – full irradiance; MI – medium irradiance; LI – low irradiance. UL – *Urena lobata* (*open bars*); BP – *Bidens pilosa* (*hatched bars*); CO – *Chromolaena odorata* (*black bars*). LN – low nitrogen; MN – medium nitrogen; HN – high nitrogen. Vertical bars represent SE of the mean (n = 5–8). Different *uppercase letters* indicate significant differences among species in the same irradiance and nitrogen conditions, while different *lowercase letters* indicate significant difference among nitrogen in the same irradiance condition of the same species according to *Duncan*'s test at p<0.05.

during invasion (Feng *et al.* 2009).

However, compared with native *U. lobata* or invasive *B. pilosa*, P_{max} of *C. odorata* was not higher, especially at FI. Thus, the invasiveness of *C. odorata* cannot be explained by P_{max} maximization theory. The lower P_{max} at FI was possibly related to its low g_s (Fig. 3*M*), which could slow down gas-exchange rate and reduce the photosynthetic rate. However, the transpiration rate can be reduced to prevent excessive loss of water and it enables plants to better adapt to high irradiance and drought. Zhang *et al.* (2009) demonstrated that *C. odorata* preferred high light or even mild drought habitats in the field. Although P_{max} of *C. odorata* was not high, its LCP was the lowest, especially at FI and MI, and it is still much lower than that of *U. lobata* at LI as long as nutrients were sufficient (Fig. 3*G–I*). A lower LCP of plants usually means a stronger ability to use low irradiance (Pattison *et al.* 1998). Thus, *C. odorata* could utilize the weak irradiance more effectively, which corresponded to the changes in the Chl *a*/*b* ratio. Similar results have been found in other invasive plants, such as *Lythrum salicaria* that invades USA. This species does not show the higher photosynthetic rate but the lower LCP than that of native plants; it gains the advantage to utilize low irradiance and facilitate seedling colonization and successful invasion (Nagel and Griffin 2004). Though LSP of *C. odorata* at FI was lower than or equal to that of *U. lobata*, it still maintained the value of 1,745.48 µmol m^{-2} s^{-1} at HN (Fig. 3*D*). According to field measurements, the highest diurnal light intensity in the summer of Southern China was mostly around 1,600 µmol(photon) m^{-2} s^{-1}. As a typical tropical weed, *C. odorata* has a lower LSP than that of *U. lobata*, but it can still use high light in the area. However, LSP of *U. lobata* declined rapidly at MI and LI condition, but the two invasive weeds decreased less, especially *C. odorata*, which was significantly higher than that of *U. lobata* in most treatments. This indicated that even in shaded environment, *C. odorata* is able to maximize utilization of light resources to accumulate more biomass by maintaining a relative high LSP intercepting more photosynthetically active radiation for its growth. Additionally, R_D of *C. odorata* was lower than that of *U. lobata* at FI–HN, indicating that less carbon was consumed by respiration and hence it was beneficial to carbon storage (Fig. 3*J*). Meanwhile, two invasive species, especially *C. odorata*, had a significantly higher WUE$_i$ than that of *U. lobata* in most treatments, which suggested higher resource-utilization efficiency and could form more productivity base on the same investment of water resource (Fig. 3*P–R*).

Although the photosynthetic rate of most invasive plants is higher, more and more studies have found that photosynthetic capacity and invasiveness of alien plants

Table 2. Mean phenotypic plasticity index (MPPI) for physiological traits of *Chromolaena odorata*, *Bidens pilosa*, and *Urena lobata* in response to nitrogen under different irradiance conditions. FI – full irradiance; MI – medium irradiance; LI – low irradiance. Chl – chlorophyll; P_{max} – light-saturated photosynthetic rate; LSP – light saturation point; LCP – light compensation point; R_D – dark respiration rate; g_s – stomatal conductance; WUE$_i$ – intrinsic water-use efficiency.

Parameter	*C. odorata*			Mean	*B. pilosa*			Mean	*U. lobata*			Mean
	FI	MI	LI		FI	MI	LI		FI	MI	LI	
Chl	0.65	0.36	0.15	0.39	0.52	0.30	0.19	0.34	0.44	0.26	0.05	0.25
P_{max}	0.42	0.24	0.32	0.32	0.45	0.43	0.27	0.38	0.57	0.32	0.21	0.37
LSP	0.43	0.27	0.42	0.37	0.29	0.48	0.23	0.34	0.63	0.50	0.31	0.48
LCP	0.39	0.33	0.16	0.29	0.43	0.19	0.34	0.32	0.52	0.30	0.31	0.38
R_D	0.42	0.50	0.27	0.40	0.43	0.28	0.27	0.33	0.65	0.49	0.49	0.55
g_s	0.17	0.25	0.18	0.20	0.31	0.59	0.28	0.39	0.66	0.26	0.31	0.41
WUE$_i$	0.27	0.36	0.25	0.29	0.37	0.10	0.40	0.29	0.29	0.34	0.42	0.35
Total				0.32				0.34				0.40

Table 3. Mean phenotypic plasticity index (MPPI) for physiological traits of *Chromolaena odorata*, *Bidens pilosa,* and *Urena lobata* in response to irradiance under different nitrogen conditions. LN – low nitrogen; MN – medium nitrogen; HN – high nitrogen. Chl – chlorophyll; P_{max} – light-saturated photosynthetic rate; LSP – light saturation point; LCP – light compensation point; R_D – dark respiration rate; g_s – stomatal conductance; WUE$_i$ – intrinsic water-use efficiency.

Parameter	*C. odorata*			Mean	*B. pilosa*			Mean	*U. lobata*			Mean
	LN	MN	HN		LN	MN	HN		LN	MN	HN	
Chl (*a*+*b*)	0.75	0.48	0.37	0.53	0.70	0.54	0.45	0.56	0.37	0.24	0.10	0.24
P_{max}	0.54	0.60	0.61	0.58	0.64	0.69	0.73	0.69	0.55	0.83	0.84	0.74
LSP	0.66	0.66	0.67	0.66	0.74	0.80	0.77	0.77	0.58	0.85	0.89	0.77
LCP	0.20	0.51	0.59	0.43	0.35	0.60	0.76	0.57	0.48	0.61	0.65	0.58
R_D	0.72	0.82	0.78	0.77	0.80	0.89	0.92	0.87	0.68	0.81	0.78	0.76
g_s	0.64	0.56	0.66	0.62	0.73	0.78	0.75	0.75	0.70	0.79	0.88	0.79
WUE$_i$	0.44	0.22	0.40	0.35	0.40	0.50	0.55	0.48	0.56	0.48	0.68	0.57
Total				0.56				0.67				0.64

cannot be fully represented by P_{max} alone (Smith and Knapp 2001, Garcia-Serrano *et al.* 2009). Our findings also showed that P_{max} of *C. odorata* was not particularly higher, but P_{max} only represented the photosynthetic capacity per unit of leaf area. *C. odorata* showed lower LCP and $R_{D,}$ suggesting that it had higher ability to utilize low irradiance in shaded environment and to decrease carbon loss by respiration during the night. Moreover, some plant traits, such as branch number, total leaf area, and specific leaf area (SLA), were significantly higher in *C. odorata* than those of native species. We found that the branch number and the total leaf area were positively and significantly correlated with relative growth rate (RGR) and biomass (unpublished data). P_{max} values shown in our study were also strongly correlated with LSP, LCP, and R_D. The higher branch number, total leaf area, LSP, and lower LCP and R_D could be helpful for accumulating more carbon at a plant level and they enhance its competitive advantage and invasiveness. In the fields, *C. odorata* can produce seeds under highly shaded habitats and even survive in the environment with only 4.5% of irradiance due to its efficient utilization of low light (Wang *et al.* 2003, Joshi *et al.* 2006). Allred *et al.* (2010) found that P_{max} of invasive *Lespedeza cuneata* is lesser than 50% of that of native *Andropogon gerardii*, and its apparent quantum yield is also lower, with poor utilization of low irradiance and no obvious photosynthetic advantage. However, total leaf area and SLA of *L. cuneata* are significantly higher than those of native plants, which means that the leaf area used for light interception and CO_2 assimilation is even higher. This characteristic can compensate for its lower photosynthetic rate to a certain extent, facilitating carbon accumulation on the plant level and successful invasion.

Phenotypic plasticity and invasiveness: Many previous studies have found that phenotypic plasticity of invasive species is higher than that of native species in the same habitat. However, such conclusions are usually based on experience in some cases, as phenotypic plasticity of plants involves morphological, physiological, and reproductive characteristics with different responses to changing environment; and even for the same trait, the responses to various environment conditions might be inconsistent (Richards *et al.* 2006, Hulme 2008, Molina-Montenegro *et al.* 2010). Besides, phenotypic plasticity of invasive plants in different geographical populations also varies significantly. In general, compared with native or noninvasive species, phenotypic plasticity of morphology and biomass allocation of invasive species is higher, but the situation might be reversed for other characteristics (Brock *et al.* 2005, Leishman *et al.* 2005, Richards *et al.* 2006, Maron *et al.* 2007, Droste *et al.* 2010). For instance, invasive *Taraxacum officinale* has a lower phenotypic plasticity in seed dispersal traits, which is conducive to invasion (Brock *et al.* 2005). The response of P_{max} and g_s in exotic *L. cuneata* to light and season is lower than that of natives, and therefore it shows high environmental tolerance and achieves a faster occupation of the new habitat (Allred *et al.* 2010).

Our findings showed that although the plasticity of the Chl (*a*+*b*) content of two invasive weeds was higher than that of *U. lobata*, their plasticity of photosynthetic parameters was lower, especially for *C. odorata*. Compared with native plants, *C. odorata* could adapt to a wider range of temperatures and be able to grow normally in a high-temperature environment and form a mono-dominated community due to maintaining the high photosynthetic rate under higher temperatures (Chen 2006). Williams *et al.* (2008) found that compared to some traits such as plant size and fruiting ability, plasticity of physiological traits of invasive plants may be lower than that of native plants. If the plasticity is too high, the fitness of the plant would be reduced sharply under unfavorable environments. A lower plasticity of these traits could compensate for the negative effects of adverse environments and facilitate an invasion. The study of invasive *Hypericum perforatum* showed also similar results (Maron *et al.* 2007). Therefore, the lower phenotypic plasticity of physiological traits, particularly of photosynthetic parameters in *C. odorata*, helps maintain a relatively stable photosynthetic capacity under larger resource range (especially in barren habitats) and thus to accumulate more biomass. This might be one of competitive strategies of *C. odorata* for its successful invasion.

In conclusion, the results presented here indicate that all three species prefer high irradiance and nutrient-rich conditions. Limited light availability under shading or limited nitrogen supply reduced the photosynthetic capability of all three weeds, although *C. odorata* developed effective mechanisms for its acclimation to medium and low irradiance. Although P_{max} of *C. odorata* was not higher than that of *U. lobata*, it could maintain the relatively high LSP and low LCP in shaded environment. These traits gave it the advantage to utilize low irradiance resources, expand the range of photosynthetically active radiation, prolong the effective time for photosynthesis, and finally facilitate biomass accumulation and plant growth. Meanwhile, the lower photosynthetic physiological plasticity of *C. odorata* in response to irradiance or nitrogen also improved the relative competitive advantages that benefited its growth. Performance of *C. odorata* decreased with the decrease of irradiance or nitrogen availability (Zhang and Wen 2009, Qin *et al.* 2013), showing that efforts to control its spreading in the fields should be mainly directed against populations in open or nutrient-rich habitats since that is where the progress of its invasion would be much faster. Deep shading by intact canopies or luxuriant forests could be an effective barrier against its invasion. Further studies including less than 15% of irradiance are necessary for detecting the effects on photosynthetic capability and invasiveness of *C. odorata.*

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