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Original article

Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels

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ABSTRACT

We tested the hypotheses that invasive species had higher irradiance plasticity, capture ability and efficiency than noninvasive species using two invasive aliens – *Ageratina adenophora* and *Chromolaena odorata*, and one noninvasive alien – *Gynura* sp. The three aliens were grown at 4.5%, 12.5%, 36%, 50% and 100% irradiances for 64 days before harvesting. The plastic response of specific leaf area (SLA) contributed to improved light interception at low irradiance, carbon gain and water balance at high irradiance. It was a good predictor for intraspecific irradiance responses of leaf area ratio (LAR), leaf area:root mass ratio, maximum photosynthetic rate (P_{max}) and net assimilation rate (NAR). Biomass allocation-related traits were species specific and their plasticity to irradiance was low. The high root mass fraction, leaf mass fraction and LAR distinguished the two invaders from *Gynura*. However, other resource capture-related traits, such as SLA, NAR and P_{max}, were not always higher for the invaders than for *Gynura*. Furthermore, plasticity to irradiance was not different between the invasive and noninvasive aliens. With increasing irradiance, *Gynura* decreased biomass investment to roots and leaves but increased the investment to support structures adversely affecting both low and high irradiance acclimation. *Ageratina* might invade new habitat successfully through tolerating shading at low irradiance and outshading competitors by forming dense stands when irradiance is increased. The results suggested that both resource capture-related traits and irradiance acclimation conferred competitive advantage to the two invaders and some traits were common for invasive and noninvasive aliens but others were specific for invaders.

1. Introduction

Identifying the factors that influence invasions by exotic plants is very important for improving prediction and control of potentially invasive species. Comparisons across phylogenetically related invasive and native species and comparisons across ecologically similar, sympatric invasive and noninvasive species are two important methods used to explore plant

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traits that are associated with invasiveness (Mack, 1996; McDowell, 2002). Most of these comparative studies have focused only on invasive exotic species (Davis et al., 2000). Few studies have compared traits of invasive aliens with those of less or noninvasive aliens (Nijs et al., 2004), indicating that the factors underlying variation in invasiveness have remained largely unidentified. A majority (ca. 90%) of successful exotic species are noninvasive (Williamson and Fitter, 1996) as they are able to establish and persist but not outcompete native species (Rejmanek, 2000).

The ability of plants to capture and utilize light is an important determinant of growth potential and fitness. Competition for light is the primary factor influencing weed invasion (Standish et al., 2001; D'Antonio et al., 2001). Generally, growth rate is higher in invasive than in native species (Witkowski and Lamont, 1991; Pattison et al., 1998; Maillet and Lopez-Garcia, 2000). Pattison et al. (1998) hypothesized that successful invasive species have other morphological and physiological traits, which increase light capture and utilization efficiency.

Leaf area ratio (LAR) is the main factor explaining the variation in growth rate among different tree and herbaceous species (Witkowski and Lamont, 1991; Pattison et al., 1998; Poorter, 1999). Specific leaf area (SLA) is another important trait regulating and controlling plant functions such as carbon assimilation and carbon allocation (Reich et al., 1997; Feng et al., 2004; Zhang and Feng, 2004). The great success of invasive species is partly attributed to thinner leaves, and therefore lower carbon cost per unit photosynthetic area (Baruch and Goldstein, 1999; Durand and Goldstein, 2001; Nagel and Griffin, 2001; Smith and Knapp, 2001). Knee and Thomas (2002) found that net assimilation rate (NAR) is higher in invasive than in native species. Invasive plants may realize success through maximizing growth by maximizing photosynthesis (Baruch and Goldstein, 1999; Durand and Goldstein, 2001). Furthermore, compared with native species, successful invasive species generally have stronger stress tolerance, can acclimate to a wider range of environmental conditions (Albert et al., 2000; Annapurna and Singh, 2003) and can use fluctuating resources better (Davis et al., 2000). Hence, greater phenotypic plasticity is likely to confer greater vigor on invasive species (Yamashita et al., 2000; Durand and Goldstein, 2001).

Invasive species have been shown to exhibit high plasticity in response to light (Niinemets et al., 2003) but there is contrary evidence available. For example, compared with native species, invasive species exhibit similar or even lower LAR (Knee and Thomas, 2002), SLA (McDowell, 2002; DeWalt et al., 2004) and light-saturated photosynthetic rate ($P_{\max}$) (Smith and Knapp, 2001; Ewe and Sternberg, 2003). In addition, higher root mass fraction (RMF) (D'Antonio et al., 2001; DeWalt et al., 2004) and lower RMF plasticity (D'Antonio et al., 2001) have been demonstrated. High RMF may adversely affect carbon gain by plants through decreasing leaf mass allocation and increasing root respiratory loss although it is beneficial to water and nutrition absorption. In this study, we hypothesize that invasive exotics will have higher irradiance capture efficiency and greater phenotypic plasticity than noninvasive exotics. The main objectives of this study are to determine: (1) how the exotic species acclimate to different irradiance levels in terms of biomass allocation, growth, and photosynthesis; (2) whether the invasive species exhibit higher irradiance plasticity, resource capture ability and efficiency, i.e. higher leaf mass fraction (LMF), LAR, SLA, $P_{\max}$ and NAR, than the noninvasive species; and (3) the relationship between integrated light acclimation ability and invasiveness.

2. Materials and methods

This study was carried out in the Xishuangbanna Tropical Botanical Garden (21°56′ N, 101°15′ E, 570 m altitude) of the Chinese Academy of Sciences in Mengla county, Yunnan province, southwest China. The mean annual temperature is 21.7 °C in this area; mean temperature of the hottest month (July) is 25.3 °C and 15.6 °C during the coolest month (January). The mean annual precipitation is 1557 mm with the dry period lasting from November until April (Feng et al., 2002).

In this study, the following three perennial exotic *Compositae* forbs were investigated. *Ageratina adenophora* (Sprengel) R.M. King and H. Robinson and *Chromolaena odorata* (L.) R.M. King and H. Robinson, native to Central and South America, have invaded much of the tropics and subtropics in the world. *Gynura* sp., native to Burma, is a less or noninvasive alien (Nijs et al., 2004), as its impact on recipient habitats is very weak in the study area. Hereafter, only generic names are used for the three studied species.

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, similar sized vigorous seedlings were transplanted singly into 15 dm^3 pottery pots. Current-year seedlings of *Chromolaena* were collected as wildings from the field and transplanted to the same type of pots. Vigorous seedlings were chosen from a partially shaded site and were selected on the same basis as sown seedlings. Pots were filled with equal proportions of river sand and forest topsoil. Forest topsoil was used to provide a substrate with a natural supply of macro- and micronutrients and the river sand provided a texture with adequate drainage and facilitated harvest of the whole plant root system, including fine roots (Poorter, 1999). All the seedlings were grown at 36% irradiance for 2 weeks, then seedlings of each species were randomly divided into five groups, 20 seedlings per group, and one group was grown under one of the five irradiances used in this study, i.e. 4.5%, 12.5%, 36%, 50%, and 100%, respectively. Seedlings were watered daily and fertilized monthly with complex fertilizer.

Irradiance levels used in this study were created by covering the shade houses with different layers of black nylon shade netting, 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 a shade house during a clear day in the summer with that in a shade house with no netting. Ten quantum sensors were used to measure PPFD with two sets of Li-1400 (Li-Cor, Lincoln, Nebraska, USA). Two sensors were installed 1 m above ground and 5 m apart in each shade house. The lower 30 cm of each shade house remained open to facilitate airflow and to reduce the potential effects of other environmental factors except irradiance.

For each species and treatment an initial harvest was carried out after seedlings had acclimated to their new light environment for 2 weeks. The final harvest was carried out 50 days after the initial harvest. For each species and treatment, five and eight individuals were used for the initial and final harvest, respectively. No growth data were provided for the 4.5% irradiance level as *Gynura* did not survive and *Ageratina* and *Chromolaena* grew very slowly and did not produce enough leaves for measurement. At the initial harvest, seedling height, total leaf area, and dry biomass of leaf, support organs (including stems, branches and petioles) and roots were determined. In addition to the above variables, at the final harvest the branch number and crown width in two perpendicular directions were measured. Leaf area was determined with Li-3000A leaf area meter (Li-Cor, Lincoln, Nebraska, USA). Plant parts were oven-dried for 48 h at 80 °C. According to Poorter (1999) and Poorter and Van der Werf (1998), the following variables were derived from the measured data: RMF, LMF, support organ mass fraction (SMF), LAR, leaf area:root mass ratio (LA:RM), SLA, mean leaf area (MLA), crown area, leaf area index (LAI), RGR, NAR, mean leaf area ratio (LAR_m), growth response coefficients of $LAR_m(GRC_{LAR_m})$ and NAR (GRC_{NAR}).

Before the final harvest, photosynthetic rate (P_n) of fully expanded leaves of five plants per species per treatment was measured with Li-6400 (Li-Cor, Lincoln, Nebraska, USA), using an open, steady-state gas analysis system. Conditions in the leaf chamber were controlled automatically by the equipment, with 360 $\mu mol\, mol^{-1}$ CO_2, 60% relative humidity and a constant temperature of 30 °C. Photosynthetic responses to light were measured using 15 different PPFD, i.e. 2000, 1500, 1000, 800, 650, 500, 400, 300, 250, 200, 150, 100, 50, 20, 0 $\mu mol\, m^{-2}\, s^{-1}$, starting from the highest PPFD. The light was provided automatically by the LED light resource of the Li-6400. Data were recorded when the leaf was illuminated for 200 s under each light step. Prior to the measurement, the leaf was placed under 1500 $\mu mol\, m^{-2}\, s^{-1}$ artificial "cold light" for 30 min in order to achieve full photosynthetic capacity. The "cold light" was provided by several metal halide lamps hanging above a glass water bath cooled with flowing tap water. The measurements were taken between 8:30 and 11:30 a.m. Following Bassman and Zwier (1991), P_{max} was calculated with the photosynthetic light response curves fitted with the following equation:

$$P_n = P_{max}\left(1 - C_0 e^{-\alpha PPFD/P_{max}}\right)$$

where α was quantum yield under low PPFD, and C_0 was the dimensionless coefficient when P_n approaches zero under low PPFD.

Plasticity indices of different variables were calculated as (maximum − minimum)/maximum (Valladares et al., 2000).

Plant morphogenetic responses to irradiance were evaluated using a two-way ANCOVA, with light treatment and species as independent variables and biomass as a covariate. All dependent variables were transformed to natural logarithms prior to analysis. Plant biomass may have differed between treatments and species by the end of the experiment so natural logarithm transformed biomass was therefore included as a co-variable in the analysis. In this way, the effects of the main factors on plant variables could be evaluated by comparing plants of a similar biomass. The interaction between species and biomass was included in the analysis, as ontogenetics trajectories may differ between species. The ANCOVA was carried out using SPPS 10.0 (SPSS Inc., Chicago, Illinois, USA) for all species and treatments (following Poorter, 1999).

3. Results

Most of the allocation and morphological variables showed curvilinear responses to irradiance, with the largest changes in the low irradiance range (Fig. 1). Both light intensity and plant species had significant effects on all of the allocation and morphological traits except light on RMF and species on LA:RM (Table 1). Plant height, LAR, MLA, and crown area were significantly co-related to biomass, but only crown area was determined by biomass. Light was the most important determinant of variations in SLA, LAR, LA:RM, while plant height, RMF, SMF, LMF, MLA, and LAI appeared to be species specific.

With the increase of irradiance, RMF increased for *Ageratina* and *Chromolaena*, but surprisingly decreased for *Gynura* (Fig. 1A). In contrast, SMF decreased for the former two species, and increased for *Gynura* (Fig. 1B). For *Gynura* LMF decreased slightly with irradiance and for *Chromolaena* it remained quite stable whereas for *Ageratina*, LMF dropped to the lowest value at intermediate irradiance (Fig. 1C). Plant height decreased with irradiance for *Ageratina* and *Gynura* (Fig. 1D) but for *Chromolaena* it increased with irradiance, and peaked at the intermediate irradiance. Branch number and LAI increased with irradiance for all species (Fig. 1E and F). Response of LAI to irradiance was irregular in *Gynura*, but its value at 100% irradiance was obviously lower than those of *Ageratina* and *Chromolaena*. For all the three species SLA, LAR, LA:RM and MLA decreased significantly with irradiance (Fig. 1G–J). Specific leaf area was the main determinant of intraspecific changes in LAR and LA:RM with irradiance. With the increase of SLA, LAR and LA:RM increased, with the largest changes in the high range of SLA (Fig. 2A and B). Among the species, *Ageratina* showed the lowest height and MLA; *Chromolaena* the lowest branch number and SLA, and the biggest MLA; *Gynura* the lowest RMF, LMF and LAR, and the highest SMF.

For all the three species, P_{max} increased sharply with irradiance until 36% irradiance, then increased more gradually (Fig. 1K). Under high irradiance, P_{max} of *Gynura* was higher than those of *Ageratina* and *Chromolaena*. Light-saturated P_n was negatively correlated with SLA (Fig. 2C).

For all the three species, LAR_m decreased with increase in irradiance, while NAR and RGR increased, but *Gynura* attained highest RGR at intermediate irradiance levels (Fig. 3A–C). Surprisingly, we did not find consistent differences in RGR among the three exotic species although *Ageratina* was much smaller than the others. The contribution of NAR to growth increased with irradiance, while that of LAR_m decreased, but the latter was higher than the former at all irradiances (Fig. 3D–F). Net assimilation rate was positively related to P_{max} and negatively to SLA (Fig. 4A and B). As with LAR, LAR_m increased with SLA (Fig. 4C). A close association between SLA and RGR was not

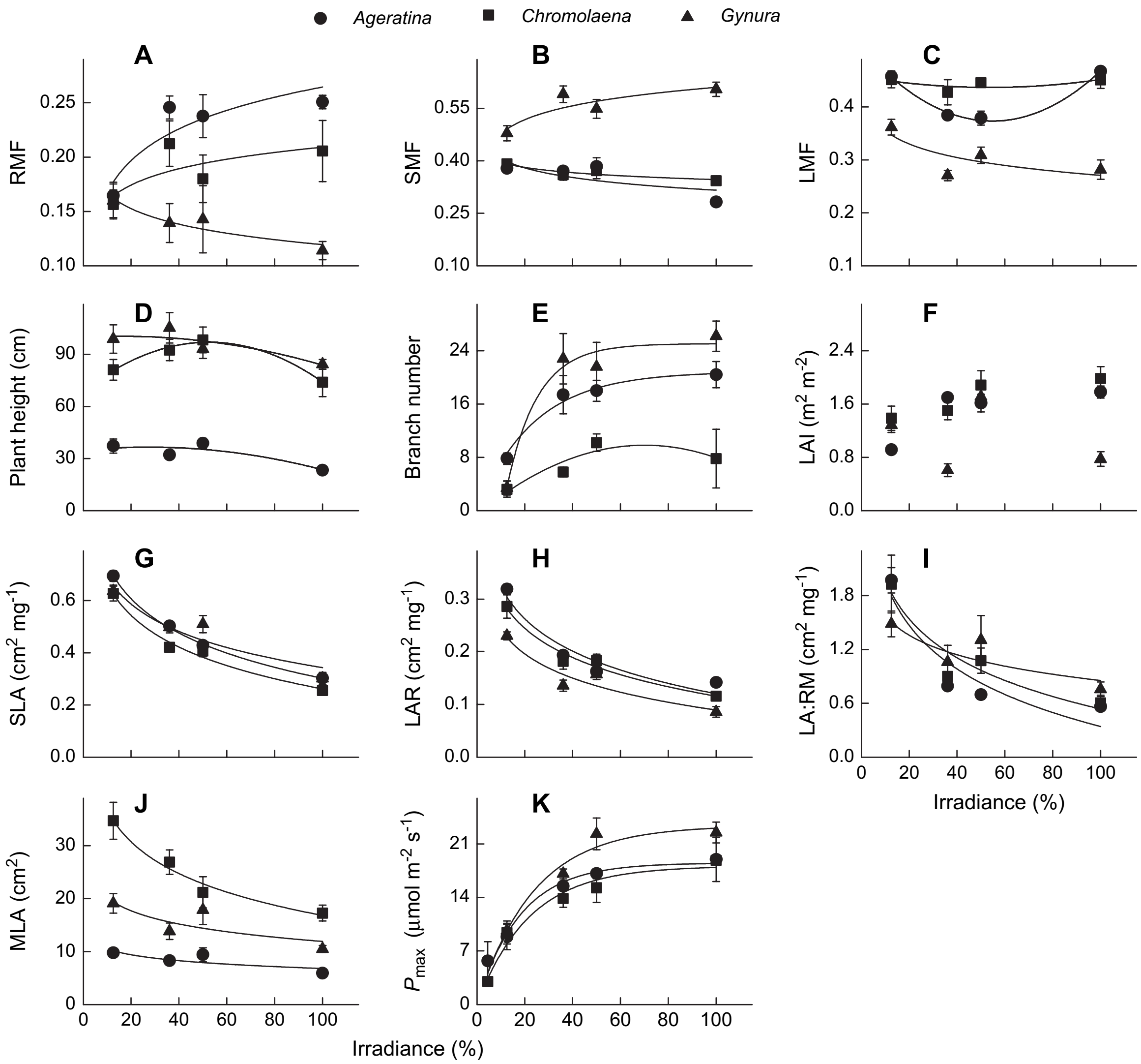

Fig. 1 – Responses to irradiance for *Ageratina adenophora*, *Chromolaena odorata* and *Gynura* sp. Mean ± SE ($n = 5$ for P_{max}, $n = 8$ for other variables). See Tables 1 and 2 for abbreviations.

found although SLA was the main determinant of P_{max}, NAR and LAR_m.

For most of the variables the interaction between irradiance and species was statistically significant (Table 1), indicating that phenotypic plasticity was significantly different among the species. Phenotypic plasticity of biomass allocation-related variables was lower than that of most other variables (Table 2). Among the three exotic species, *Chromolaena* showed the lowest plasticity indices in RMF, SMF, LMF and LAI, while *Gynura* exhibited the lowest plasticity indices in height, SLA and LA:RM.

4. Discussion

High LAR, LMF and RMF may be more relevant for explaining the invasiveness of the two invaders. Pattison et al. (1998) found that under low irradiance LAR is 20% higher in invaders than in natives. In this study, the lower LMF of *Gynura* could not be ascribed to the high plant height although LMF might decrease with height. *Chromolaena* was much taller than *Ageratina*, but its LMF was not lower than that of *Ageratina*. Furthermore, species was the main determinant of LMF. D'Antonio et al. (2001) found that invaders have higher RMF than natives. However, Pattison et al. (1998) did not find consistent differences between invasive and native species in the ratio of root to shoot. There is a trade-off between below- and aboveground resources' capture efficiency. High RMF can facilitate nutrient and water uptake, while influence light interception and utilization. Maybe RMF should be maintained in adequate scales according to environmental conditions. The RMF of the two invasive species was not higher than that of other light-demanding species (Poorter, 1999). Other resources capture-related traits, such as SLA, P_{max} and NAR may be less relevant with invasiveness of the two invasive species. High SLA might be a common attribute for exotic species. Smith and Knapp (2001) also found that SLA is not different between invasive and noninvasive exotics, but significantly higher than natives.

Table 1 – Results of a two-way ANCOVA with irradiance ($n = 4$) and species ($n = 3$) as independent variables and natural log-transformed biomass as a co-variable

Variables	Irradiance	Species	Biomass	Irradiance × species	r^2
Allocation					
RMF	1.03	**13.37*****	0.42	2.43*	0.57
SMF	4.47**	**113.69*****	4.02	7.46***	0.89
LMF	3.45*	**105.43*****	1.94	4.19**	0.87
Architecture					
Height	20.92***	**140.23*****	20.85***	3.83*	0.95
Branch number	4.62**	4.151*	3.95	**5.78****	0.82
Crown area	21.19***	6.49**	**51.81*****	8.31***	0.87
LAI	6.73***	**23.08*****	0.24	10.69***	0.75
Morphology					
SLA	**109.02*****	10.93***	3.89	2.36*	0.93
LAR	**43.11*****	16.33***	4.74*	2.53*	0.89
LA:RM	**11.46*****	1.66	0.24	2.88*	0.69
MLA	18.69***	**59.20*****	7.96**	0.89	0.87

RMF, root mass fraction ($g\,g^{-1}$); SMF, support mass fraction ($g\,g^{-1}$); LMF, leaf mass fraction ($g\,g^{-1}$); height (cm); crown area (cm^2); LAI, leaf area index ($m\,m^{-2}$); SLA, specific leaf area ($cm^2\,mg^{-1}$); LAR, leaf area ratio ($cm^2\,mg^{-1}$); LA:RM, leaf area:root mass ($cm^2\,mg^{-1}$); MLA, mean leaf area (cm^2).

The dependent variables were natural log-transformed prior to analysis. The *F*-value of each variable given in bold is the corresponding factor that is the main determinant of the variable. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

The results suggested that other traits (such as good irradiance acclimation) besides resources capture-related traits may also confer competitive advantage to the invaders (Maillet and Lopez-Garcia, 2000; Smith and Knapp, 2001).

The three exotics showed relatively high phenotypic plasticity, which is a common characteristic of light-demanding species (Feng et al., 2004). It had been hypothesized that enhanced phenotypic plasticity could play an important role in successful colonization of new habitats by exotic species (Williams et al., 1995; Yamashita et al., 2000; Durand and Goldstein, 2001; Annapurna and Singh, 2003). However, in this study, differences in phenotypic plasticity between invasive and noninvasive aliens were not found, indicating that exotic species with high phenotypic plasticity, just as in the case of *Gynura*, was not always an invasive species.

In contrast to both invaders, *Gynura* could not acclimate adequately to irradiance in term of biomass allocation. At high irradiance, decreasing RMF can induce water stress as suggested by higher LA:RM; increasing biomass allocation to branch with less leaves inevitably increases respiratory load by decreasing LMF, i.e. by increasing the ratio of non-photosynthetic organs to photosynthetic organs (Matsumoto et al., 2000). The high NAR and P_{max} of *Gynura* did not offset the negative effect of low LAR on RGR (Fig. 3C), as LAR_m was the main determinant of RGR (Fig. 3F). Increasing SMF could increase seed production at high irradiance since the apical bud of each branch would differentiate into a flower bud and then produce seeds. *Gynura* may require a trade-off between seed production and growth or water uptake. Trade-off between current reproduction and growth has been well documented (McDowell and Turner, 2002). Even so, seed production of *Gynura* was still much lower than that of *Chromolaena* and *Ageratina* (personal observation), which might partially be associated with its weak invasiveness.

At low irradiance, the increased RMF of *Gynura* is evidently not associated with transpiration demand, but maybe associated with increasing belowground carbon storage (Poorter and Rose, 2005). The increased RMF enhanced roots' respiratory losses and therefore decreased the shade tolerance of the whole plant, which at least partially explained why *Gynura*

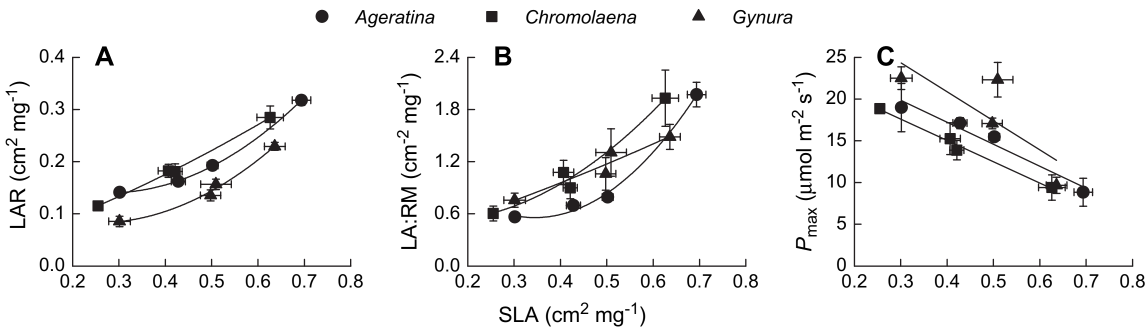

Fig. 2 – LAR, LA:RM, P_{max} as a function of SLA for *Ageratina adenophora*, *Chromolaena odorata* and *Gynura* sp. grown at four irradiance levels. Mean ± SE ($n = 5$ for P_{max}, $n = 8$ for other variables). See Tables 1 and 2 for abbreviations.

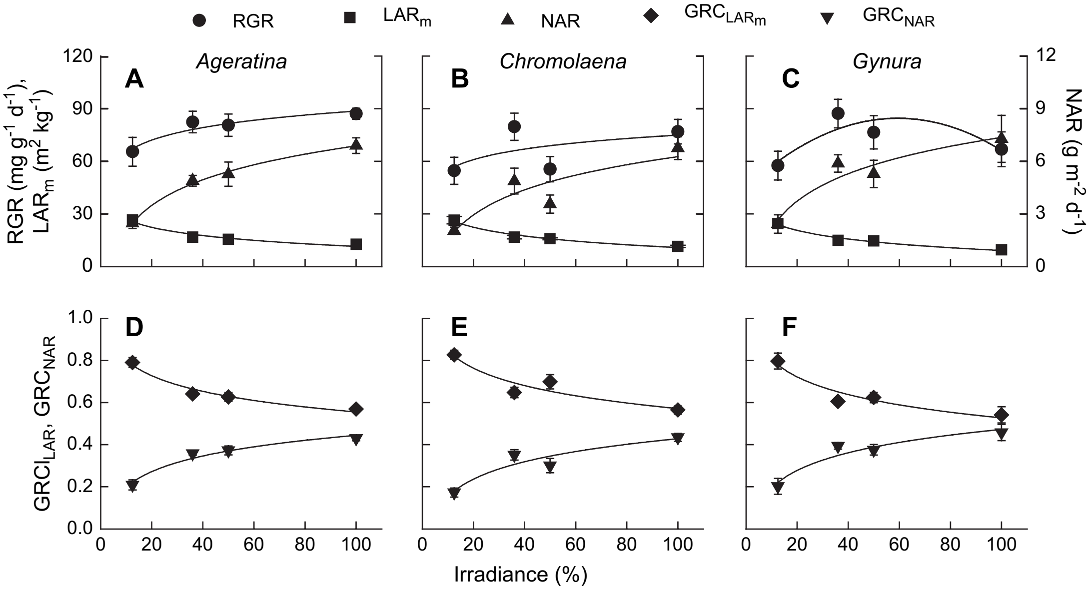

Fig. 3 – Relative growth rate (RGR), mean leaf area (LAR_m), net assimilation rate (NAR), and the contribution of LAR_m and NAR (GRC_{LAR_m} and GRC_{NAR}) to RGR for *Ageratina adenophora*, *Chromolaena odorata* and *Gynura* sp. grown at four irradiance levels. Mean ± SE ($n = 8$).

did not survive at 4.5% irradiance. The results indicated that the ability to acclimate to both low and high irradiance might be important for invasiveness of exotic plants.

Compared with *Chromolaena* and *Gynura*, the leaves of *Ageratina* were arranged in a smaller space at 100% irradiance because of its higher LAI and lower height, leading to much higher leaf densities in crown (leaf area or leaf number per unit crown volume) and higher levels of self-shading. For example, at 100% irradiance, leaf area (m^2) and leaf number per meter cube crown were 3–8 and 2–15 times greater for *Ageratina* and *Chromolaena* than for *Gynura*, respectively. Self-shading in *Ageratina* did not result in decrease in NAR and RGR. Fast leaf formation and high P_{max} would contribute to improving whole plant level carbon gain in high light environment and offset any reduction in assimilation due to self-shading (Hikosaka et al., 1994; Ackerly and Bazzaz, 1995; Yamashita et al., 2002). *Ageratina* showed strong shade-tolerant ability, it could survive and maintain relative high P_{max} at 4.5% irradiance. In field we also found that *Ageratina* could survive at 2% light regimes. Shade-tolerant ability is of prime importance for *Ageratina* because its seedlings are located at a low layer of community in the early stage of invasion. In addition, the rate of seed germination of *Ageratina* is low and seedling growth is slow. The mean height at harvest of this species was much lower than that of *Gynura* although it was sown more than 2 months earlier.

When irradiance increases after disturbance, *Ageratina* can increase growth rate and form dense crowns and stands which out shades competitors. In the field, *Ageratina* can form mono-dominated communities; light under its canopy is very low, only about 1.8% irradiance in Yunnan province, southwest China (personal observation). This creates unfavorable light conditions for other plants. Hoffmann et al. (2004) found that the abundance of native species in the ground layer is negatively related to community LAI and to the presence of invasive species. Shade tolerance is important for invasive species (Yamashita et al., 2002; Niinemets et al., 2003). Competition for light is often cited as the primary mechanism for

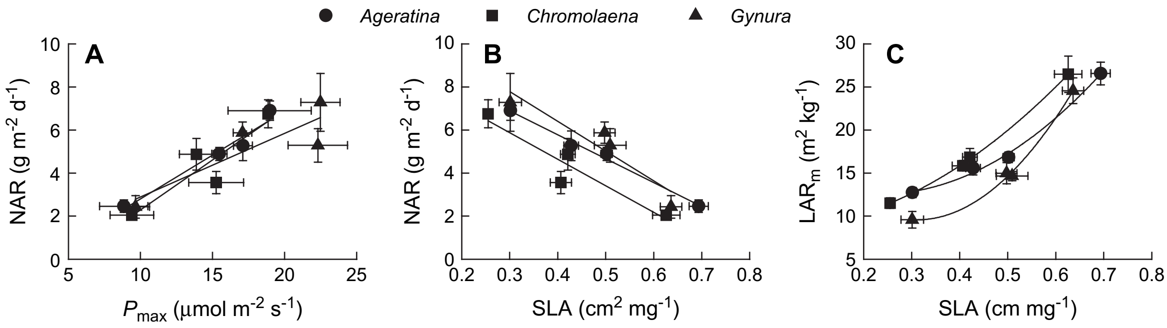

Fig. 4 – NAR as a function of P_{max} and NAR, and LAR_m as a function of SLA for *Ageratina adenophora*, *Chromolaena odorata* and *Gynura* sp. grown at four irradiance levels. Mean ± SE ($n = 5$ for P_{max}, $n = 8$ for others). See Tables 1 and 2 for abbreviations.

Table 2 – Phenotypic plasticity indices, (maximum − minimum)/maximum, for *Ageratina adenophora*, *Chromolaena odorata* and *Gynura* sp. grown at four irradiance levels

Variables	*Ageratina*	*Chromolaena*	*Gynura*
Allocation			
RMF	0.34	0.26	0.29
SMF	0.27	0.08	0.21
LMF	0.19	0.04	0.25
Architecture			
Height	0.41	0.25	0.20
Branch number	0.62	0.69	0.87
LAI	0.49	0.30	0.65
Morphology			
SLA	0.57	0.60	0.53
LAR	0.56	0.60	0.63
LA:RM	0.71	0.69	0.49
MLA	0.40	0.50	0.45
Physiology			
NAR	0.65	0.68	0.67
P_{max}	0.53	0.51	0.57
Mean	0.48	0.43	0.48

NAR, net assimilation rate ($g\,m^{-2}\,d^{-1}$); P_{max}, light-saturated photosynthetic rate ($\mu mol\,m^{-2}\,s^{-1}$); other abbreviations, see Table 1.

changes after invasion yet resulting in shading of native plants by invasive species (Standish et al., 2001; D'Antonio et al., 2001).

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REFERENCES

Ackerly, D.D., Bazzaz, F.A., 1995. Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. Oecologia 101, 289–298.

Albert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. Evol. Syst. 3, 52–66.

Annapurna, C., Singh, J.S., 2003. Variation of *Parthenium hysterophorus* in response to soil quality: implications for invasiveness. Weed Res. 43, 190–198.

Baruch, Z., Goldstein, G., 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia 121, 183–192.

Bassman, J., Zwier, J.C., 1991. Gas exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa* × *P. deltoides* clone. Tree Physiol. 8, 145–159.

D'Antonio, C.M., Hughes, R.F., Vitousek, P.M., 2001. Factors influencing dynamics of invasive C4 grasses in Hawaiian woodland, role of resource competition and priority effects. Ecology 82, 89–104.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities, a general theory of invasibility. J. Ecol. 88, 528–534.

DeWalt, S.J., Denslow, J.S., Hamrick, J.L., 2004. Biomass allocation, growth, and photosynthesis of genotypes from native and introduced ranges of the tropical shrub *Clidemia hirta*. Oecologia 138, 521–531.

Durand, L.A., Goldstein, G., 2001. Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126, 345–354.

Ewe, S.M.L., Sternberg, L.S.L., 2003. Seasonal exchange characteristics of *Schinus terebinthifolius* in a native and disturbed upland community in Everglade National Park, Florida. For. Ecol. Manag. 179, 27–36.

Feng, Y.L., Cao, K.F., Feng, Z.L., 2002. Thermal dissipation, leaf rolling and inactivation of PSII reaction centers in *Amomum villosum* in diurnal course. J. Trop. Ecol. 18, 865–876.

Feng, Y.L., Cao, K.F., Zhang, J.L., 2004. Photosynthetic characteristics, dark respiration, and leaf mass per unit area in seedlings of four tropical tree species grown under three irradiances. Photosynthetica 42, 431–437.

Hikosaka, K., Terashima, I., Katoh, S., 1994. Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. Oecologia 97, 451–457.

Hoffmann, W.A., Lucatelli, V.M.P.C., Silva, F.J., Azeuedo, I.N.C., Marinho, M.D.S., Albuquerque, A.M.S., Lopes, A.D.O., Moreira, S.P., 2004. Impact of the invasive alien grass *Melinis minutiflora* at the savanna–forest ecotone in the Brazilian Cerrado. Divers. Distrib. 10, 99–103.

Knee, M., Thomas, L.C., 2002. Light utilization and competition between *Echinacea purpurea*, *Panicum virgatum* and *Ratibida pinnata* under greenhouse and field conditions. Ecol. Res. 17, 591–599.

Mack, R.N., 1996. Predicting the identity and fate of plant invaders, emergent and emerging approaches. Biol. Conserv. 78, 107–121.

Maillet, J., Lopez-Garcia, C., 2000. What criteria are relevant for predicting the invasive capacity of a new agricultural weed? The case of invasive American species in France. Weed Res. 40, 11–26.

Matsumoto, J., Muraoka, H., Washitani, I., 2000. Whole plant carbon gain of an endangered herbaceous species *Aster kantoensis* and the influence of shading by an alien grass *Eragrostis curvula* in its gravelly floodplain habitat. Ann. Bot. 86, 787–797.

McDowell, S.C.L., 2002. Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). Am. J. Bot. 89, 1431–1438.

McDowell, S.C.L., Turner, D.P., 2002. Reproductive effort in invasive and non-invasion *Rubus*. Oecologia 133, 102–111.

Nagel, J.M., Griffin, K.L., 2001. Construction cost and invasive potential: comparing *Lythrum salicaria* (Lythraceae) with co-occurring native species along pond banks. Am. J. Bot. 88, 2252–2258.

Niinemets, Ü., Valladares, F., Ceulemans, R., 2003. Leaf-level phenotypic variability and plasticity of invasive *Rhododendron ponticum* and non-invasive *Ilex aquifolium* co-occurring at two contrasting European sites. Plant Cell Environ. 26, 941–956.

Nijs, I., Milbau, A., Seidlova, L., 2004. New methodologies for analyzing and predicting alien plant invasion from species and ecosystem traits. Weed Technol. 18, 1240–1245.

Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rain-forest species. Oecologia 117, 449–459.

Poorter, H., Van der Werf, A., 1998. Is inherent variation in RGR determined by LAR at low light and by NAR at high light? In: Lambers, H., Poorter, H., Van Vuuren, M.M.I. (Eds.), Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Backhuys Publishers, Leiden, Holland, pp. 309–336.

Poorter, L., 1999. Growth responses of 15 rain forest tree species to a light gradient: the relative importance of morphological and physiological traits. Funct. Ecol. 13, 396–410.

Poorter, L., Rose, S.A., 2005. Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. Oecologia 142, 378–387.

Reich, P.B., Walters, M.B., Ellsworth, D., 1997. From tropics to tundra, global convergence in plant functioning. Proc. Natl. Acad. Sci. U.S.A. 94, 13730–13734.

Rejmanek, M., 2000. Invasive plants, approaches and prediction. Aust. J. Ecol. 25, 497–506.

Smith, M.D., Knapp, A.K., 2001. Physiological and morphological traits of exotic, invasive exotic and native species in tallgrass prairie. Int. J. Plant Sci. 162, 785–792.

Standish, R.J., Robertson, A.W., Williams, P.A., 2001. The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. J. Appl. Ecol. 38, 1253–1263.

Valladares, F., Wright, S.J., Lasso, E., Kitajima, K., Peatcy, R.W., 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81, 1925–1936.

Williams, D.G., Mack, R.N., Black, R.A., 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. Ecology 76, 1569–1580.

Williamson, M., Fitter, A., 1996. The varying success of invaders. Ecology 77, 1661–1666.

Witkowski, E.T.F., Lamont, B.B., 1991. Leaf specific mass confounds leaf density and thickness. Oecologia 88, 486–493.

Yamashita, N., Ishida, A., Kushima, H., Tanaka, N., 2000. Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. Oecologia 125, 412–419.

Yamashita, N., Koike, N., Ishida, A., 2002. Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status. Plant Cell Environ. 25, 1341–1356.

Zhang, Y.J., Feng, Y.L., 2004. The relationships between photosynthetic capacity and lamina mass per unit area, nitrogen content and partitioning in seedlings of two *Ficus* species grown under different irradiance. J. Plant Physiol. Mol. Biol. 30, 269–276.