Physiological and morphological responses of invasive *Ambrosia artemisiifolia* (common ragweed) to different irradiances

Zhong Qin, Dan Juan Mao, Guo Ming Quan, Jia-en Zhang, Jun Fang Xie, and Antonio DiTommaso

**Abstract:** Invasion by the exotic herb *Ambrosia artemisiifolia* L. has become a serious agricultural and environmental problem and of increasing research interest as the species continues its southward spread into subtropical regions of China. To better understand the possible physiological and morphological adaptations of *A. artemisiifolia* in this region, we conducted a greenhouse experiment using seedlings of *A. artemisiifolia* and a comparative native species, *Urena lobata* L. (Caesar’s weed), which is an erect annual shrub in the Malvaceae that commonly co-occurs with *A. artemisiifolia* in open, disturbed habitats in southern China. Seedlings of both plants were grown under four irradiance regimes (10%, 30%, 55%, and 100% irradiance) from 14 May to 13 July 2010. *Ambrosia artemisiifolia* showed significantly higher total biomass, total leaf area, specific leaf area, relative growth rate, and net assimilation rate but lower leaf mass fraction than *U. lobata* at the 30%–100% irradiance levels. With decreasing irradiance, *A. artemisiifolia* significantly increased biomass allocation to stems and decreased allocation to roots. Meanwhile, *A. artemisiifolia* exhibited higher light-saturated photosynthetic rates and light saturation points with wide variances except at the 10% irradiance treatment. These findings suggest that *A. artemisiifolia* has generally higher irradiance plasticity for traits pertaining to biomass partitioning, growth, and plant structure than *U. lobata*. The ability of *A. artemisiifolia* to tolerate high shade conditions while maintaining high growth rates at elevated irradiance levels may afford it a competitive advantage and may help explain its recent colonization and spread in southern China.

**Key words:** irradiance acclimation, morphology, photosynthesis, adaptation, plasticity, China, distribution.

**Mots-clés :** acclimatation à l’irradiance, morphologie, photosynthèse, adaptation, plasticité, Chine, distribution.

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Introduction

The deleterious ecological impacts of exotic invasive plants on the stability and structure of native ecosystems has received increasing research attention (Zavaleta et al. 2001; Broennimann and Guisan 2008; Weidenhamer and Callaway 2010). Much work has also been focused on determining what plant traits may favor growth and spread of invasive species into new regions (Thorpe et al. 2009; Colautti et al. 2010). Characteristics of invasive plants identified to facilitate their establishment and dominance in newly colonized habitats include high resource capture ability, use efficiency, and enhanced phenotypic plasticity (Durand and Goldstein 2001; Schumacher et al. 2009). Light availability is the most important resource for plants and influences both vegetative and reproductive growth (Chazdon and Pearcy 1986). Many successful invasive species exhibit higher relative growth rates (RGR), specific leaf area (SLA), and leaf area ratio (LAR) than native species (Nagel and Griffin 2001; Zhao and Chen 2011). In response to decreasing irradiance, some of these invasive species also exhibit biomass allocation patterns that promote light capture by allocating more biomass to leaves and less to roots than native species (Ewe and Silveira Lobo Sternberg 2005; Feng et al. 2007a). Invasive species have been found to generally show higher photosynthetic capacity and plasticity relative to native species as they acclimate to varying light or other environmental conditions (Lin and Hsu 2004; McAlpine et al. 2008). Despite increased research on determining which plant ecophysiological and ecological traits may favor some species becoming invasive in new regions (Pyšek and Richardson 2007; Gomulkiewicz et al. 2010), there is a paucity of information on the possible underlying mechanism(s) contributing to the invasive success of Ambrosia artemisiifolia L. (common ragweed) in southern China since it was first identified and reported in 2002 (Zeng et al. 2009).

Ambrosia artemisiifolia (Asteraceae) is an invasive herbaceous annual native to eastern North America that has recently become troublesome in several regions of the world, especially central and eastern Europe and China (Chrenová et al. 2010; Kasprzyk et al. 2011). Ambrosia artemisiifolia was first introduced into China in the 1930s, but it was not until the last three decades that the species rapidly and aggressively spread into new regions of China where it is considered a serious threat to agricultural production and human health (Li et al. 2009; Deng et al. 2010). Its current range in China extends from northeastern temperate regions (49°N) to southeastern, subtropical coastal regions (24°N), thus extending over a broad environmental and ecological range. One possible explanation for the rapid expansion and spread of A. artemisiifolia in southern China may be its adaptation to varying environmental conditions, as well as to its high resource capture ability and use efficiency. This ability to quickly adapt to different environmental conditions, especially the high light environments typically found in subtropical China, may be particularly favourable for this exotic species and warrants further study.

To explore the irradiance acclimation potential of A. artemisiifolia, we performed a greenhouse study using established seedlings of A. artemisiifolia and a frequently co-occurring native in open, disturbed habitats, Urena lobata L. (Caesar’s weed, Malvaceae), grown at four irradiance levels. The objectives of the study were as follows: (i) to determine plant growth, leaf mor-
including plant and stem height, number of leaves and branches, and branch length. The plants from each replicate were then divided into leaves, stems plus petioles, and roots and dried separately to constant mass (±0.1 mg) at 85 °C. Leaf area was determined with a LI-3000A leaf area meter (LI-COR, Lincoln, Nebraska) before drying. The raw data were used to calculate the following growth parameters (Poorter 1999): leaf mass fraction (LMF), root mass fraction (RMF), support organ mass fraction (SMF), SLA, LAR, RGR, and net assimilation rate (NAR). The crown area (CA), leaf area index (LAI), root-to-shoot ratio (RSR), root-to-crown ratio (RCR), and leaf area to root mass ratio (LAR:RM) were also determined (Poorter and Werf 1998). Total above- and below-ground biomass were used to assess plant performance (Givnish 2002).

From 9 to 13 July 2010, responses of net CO₂ assimilation to PPFD were measured on sunny days with a portable photosynthesis system with a fluorescence chamber (LI6400; LI-COR, Lincoln, Nebraska) between 0900 and 1100 local time. Fully expanded sun leaves from five to eight healthy individuals of each species and irradiance treatment were sampled. Light response curves were produced by measuring photosynthesis in the following order: 2000, 1500, 1000, 800, 600, 400, 200, 150, 100, 80, 50, 20, and 0 µmol·m⁻²·s⁻¹ under fixed air flow rate (0.5 L·min⁻¹) and leaf temperature (25 ± 1 °C). Each leaf was kept for 3 min at the same light intensity in the leaf chamber. The maximum radiant energy saturated photosynthetic rate (Pₚₘₓ) was calculated according to the photosynthetic light response curves fitted with the following exponential equation (Bassman and Zwier 1991):

\[ P_n = P_{max}(1 - c_0 e^{-aPPFD/P_{max}}) \]

where \( P_n \) is the photosynthetic rate (µmol CO₂·m⁻²·s⁻¹), \( P_{max} \) is the maximum radiant energy photosynthetic rate (µmol CO₂·m⁻²·s⁻¹), \( c_0 \) is quantum yield under low PPFD, and \( a \) is the dimensionless coefficient when \( P_n \) approaches zero under low PPFD. The light saturation point (LSPT) was obtained as the lowest value of PAR for which photosynthesis reached 90% of \( P_{max} \), and the light compensation point (LCPT) was calculated when the photosynthetic rate approached zero. Dark respiration (\( R_d \)) was derived from linear regression of the first five points (0–200 µmol·m⁻²·s⁻¹) of each replicate curve (Alpert et al. 2000). Parameters of the model were calculated by the nonlinear estimation module of SPSS (SPSS version 17.0 for Windows; SPSS Inc., Chicago, Illinois). The index of phenotypic plasticity was calculated as the difference between the minimum and maximum values of the treatment means of a trait divided by the maximum values (Valladares and Pearcy 1997).

**Statistical analysis**

Differences between \( A. \) artemisiifolia and \( U. \) lobata for a given trait were evaluated with interaction terms (species × irradiance) in a nested ANOVA or ANCOVA with species nested within irradiance level. Differences among the four irradiances for the same species were analyzed with ANOVA, and a post hoc test (Duncan’s multiple range test) was performed if the differences were significant (\( p < 0.05 \)). Differences between the two species for a given irradiance level were detected with an independent samples \( t \) test. The Mann–Whitney \( U \) test was used to examine differences in phenotypic plasticity. Regression analyses for measured responses were performed with multiple models to determine the best predictive equation for each study species. All statistical analyses were carried out using SPSS 17.0.

**Results**

**Morphological responses to irradiance**

Both \( A. \) artemisiifolia and \( U. \) lobata plants had high survivorship in the different irradiance regimes. Irradiance had a profound effect on all traits (except for SMF), whereas species significantly affected traits, including SMF, LMF, NAR, LAR, and leaf and crown area (Table 1 and Table 2). There were also significant interactions between irradiance and species in SMF, RGR, NAR, LAR, and SLA. Species was the main determinant of SMF, LMF, leaf number, and number and length of first branches, whereas other variables were mainly determined by irradiance level.

For both species, the number of leaves and branches, LAI, and basal width of stems increased significantly with increasing irradiance level. \( A. \) artemisiifolia had a significantly higher number of leaves and branches than \( U. \) lobata at each of the four irradiance levels. Plant height for the two species increased from the 10% irradiance level to the 55% level, but decreased when irradiance increased to the 100% level. There were significant differences in plant height, both among the four irradiance treatments and between the two species. Plant heights of \( A. \) artemisiifolia exceeded those of \( U. \) lobata by 24.0%–92.6% at the 30%–100% irradiance levels. Mean plant height reached 136.3 cm at the 55% irradiance level, about 1.4-fold higher than the maximum height attained by \( U. \) lobata at the 30% irradiance level. However, at the 10% irradiance level, the height of \( A. \) artemisiifolia plants was 31.6% lower than the height of \( U. \) lobata plants (Fig. 1).

Both total biomass and leaf area increased significantly with increasing light intensity. When compared with plants subjected to the 10% irradiance treatment, \( A. \) artemisiifolia and \( U. \) lobata plants grown in full sunlight had 14-fold and 2.3-fold greater leaf area and produced 26.8-fold and 4.2-fold greater total biomass, respectively. Total biomass and leaf area of \( A. \) artemisiifolia grown under relatively higher irradiance conditions (above 10% irradiance) were 61%–86% and 3%–49% higher, respectively, than for \( U. \) lobata. In contrast, \( A. \) artemisiifolia showed a substantial decrease in total biomass (71.8%) and leaf area (75.6%) in deep shade (10% irradiance) compared with \( U. \) lobata, suggesting significant differences in the responses of the two species to the different light intensities.

SLA varied between \( A. \) artemisiifolia and \( U. \) lobata, with a significant interaction between the two species. SLA was higher for \( A. \) artemisiifolia in the 30%, 55%, and 100% irradiance treatments, although values were not significantly different between the two species at the 30% irradiance level. Within species, SLA decreased significantly with increasing irradiance level. Mean LAR in \( A. \) artemisiifolia and \( U. \) lobata decreased markedly with increasing irradiance, with significant differences detected at the 10% and 30% irradiance levels. \( A. \) artemisiifolia had a lower LAR than \( U. \) lobata except at the 100% irradiance level.

Both species experienced significant decreases in root biomass allocation with decreasing irradiance, though differences
### Table 1. Summary of nested ANCOVA analysis of effects of target species \((n = 2)\), irradiance level \((n = 4)\), biomass, and their interactions on traits related to plant biomass allocation and growth. Also shown are calculated plasticity indices for *Ambrosia artemisiifolia* (A.a.) and *Urena lobata* (U.l.) in response to the irradiance treatments.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Species</th>
<th>Irradiance</th>
<th>Biomass</th>
<th>Interaction</th>
<th>Plasticity index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(F)</td>
<td>(R^2)</td>
<td>(R^2)</td>
<td>A.a.</td>
</tr>
<tr>
<td><strong>Biomass allocation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RMF (%)</td>
<td></td>
<td>0.06</td>
<td>0.81</td>
<td>0.09</td>
<td>0.95</td>
</tr>
<tr>
<td>SMF (%)</td>
<td></td>
<td>0.83</td>
<td>0.37</td>
<td>1.85</td>
<td>11.26</td>
</tr>
<tr>
<td>LMF (%)</td>
<td></td>
<td>0.61</td>
<td>0.44</td>
<td>1.12</td>
<td>19.36</td>
</tr>
<tr>
<td>RCR (%)</td>
<td></td>
<td>0.43</td>
<td>0.52</td>
<td>0.80</td>
<td>0.49</td>
</tr>
<tr>
<td>RSR (%)</td>
<td></td>
<td>0.91</td>
<td>0.35</td>
<td>1.93</td>
<td>0.34</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Note:** \( F \) values, levels of significance \((p)\), total \( R^2 \) of the model, and plasticity indices are shown. \( R^2_s, R^2_b, R^2_I \), and \( R^2_{sb} \) were calculated as the sum of squares of the effect (main effects, co-variable effects (irradiance and biomass), and interactions in proportion to the total sum of squares, respectively). RMF, root mass fraction; SMF, support organ mass fraction; LMF, leaf mass fraction; RCR, root-to-crown ratio; RSR, root-to-shoot ratio; RGR, relative growth rate; NAR, net assimilation rate.

### Table 2. Summary of nested ANCOVA analysis of effects of target species \((n = 2)\), irradiance level \((n = 4)\), and their interactions on traits related to plant morphology. Also shown are calculated plasticity indices for *Ambrosia artemisiifolia* (A.a.) and *Urena lobata* (U.l.) in response to the irradiance treatments.

<table>
<thead>
<tr>
<th>Morphological trait</th>
<th>Species</th>
<th>Irradiance</th>
<th>Interaction</th>
<th>Plasticity index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(F)</td>
<td>(R^2)</td>
<td>(R^2)</td>
</tr>
<tr>
<td>PH (cm)</td>
<td>31.46</td>
<td>0.00</td>
<td>20.34</td>
<td>15.58</td>
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<tr>
<td>WBS (cm)</td>
<td>3.83</td>
<td>0.06</td>
<td>5.29</td>
<td>14.38</td>
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<tr>
<td>CW (cm)</td>
<td>0.67</td>
<td>0.42</td>
<td>0.84</td>
<td>16.46</td>
</tr>
<tr>
<td>CA (cm^2)</td>
<td>0.11</td>
<td>0.75</td>
<td>0.16</td>
<td>12.19</td>
</tr>
<tr>
<td>NI</td>
<td>17.93</td>
<td>0.00</td>
<td>30.07</td>
<td>3.92</td>
</tr>
<tr>
<td>NFB</td>
<td>190.17</td>
<td>0.00</td>
<td>65.04</td>
<td>20.12</td>
</tr>
<tr>
<td>LFB (cm)</td>
<td>1.60</td>
<td>0.22</td>
<td>2.07</td>
<td>15.13</td>
</tr>
<tr>
<td>NL</td>
<td>219.68</td>
<td>0.00</td>
<td>50.18</td>
<td>46.11</td>
</tr>
<tr>
<td>LA (cm^2)</td>
<td>7.66</td>
<td>0.01</td>
<td>3.80</td>
<td>32.91</td>
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<tr>
<td>LAI</td>
<td>0.74</td>
<td>0.40</td>
<td>1.10</td>
<td>6.08</td>
</tr>
<tr>
<td>LAR (cm^2·g^-1)</td>
<td>21.82</td>
<td>0.00</td>
<td>11.40</td>
<td>41.34</td>
</tr>
<tr>
<td>LA:RM</td>
<td>0.73</td>
<td>0.40</td>
<td>0.53</td>
<td>35.49</td>
</tr>
<tr>
<td>SLA (cm^2·g^-1)</td>
<td>0.12</td>
<td>0.73</td>
<td>0.20</td>
<td>8.44</td>
</tr>
<tr>
<td>LMA (mg·cm^-2)</td>
<td>0.89</td>
<td>0.36</td>
<td>1.33</td>
<td>7.51</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Note:** \( F \) values, levels of significance \((p)\), total \( R^2 \) of the model, and plasticity indices are shown. \( R^2_s, R^2_b, R^2_I \), and \( R^2_{sb} \) were calculated as the sum of squares of the effect (main effects and interactions in proportion to the total sum of squares, respectively). PH, plant height; WBS, width of basal stem; CW, crown width; CA, crown area; NI, number of internodes; NFB, number of first branches; LFB, length of first branches; NL, number of leaves; LA, leaf area; LAI, leaf area index; LAR, leaf area ratio; LA:RM, ratio of leaf area to root mass; SLA, specific leaf area; LMA, leaf dry matter per leaf area.

in RMF between the species at each irradiance level were not statistically significant. Stem and leaf biomass allocation were significantly different across irradiance treatments and between species. Both species showed significant increasing trends in SMF and LMF with decreasing irradiance intensity, especially for *A. artemisiifolia*. For instance, *A. artemisiifolia* grown at the 10% irradiance and full sunlight levels allocated a mean of 44.7% and 58.2% of total biomass to stems, respectively, whereas *U. lobata* allocated a mean of 33.4% and 46.2% of total biomass to stems, respectively, at similar irradiance levels. For LMF, *A. artemisiifolia* allocated a significantly lower fraction of total biomass to leaves compared with *U. lobata* under the same irradiance conditions. For instance, mean LMF of *A. artemisiifolia* was 19.4% in full sunlight, whereas it amounted to 28.8% for *U. lobata*. *Ambrosia artemisiifolia* allocated most of its biomass to stems and less to foliage.

Shade induced significantly higher RCR relative to full sun in both *A. artemisiifolia* and *U. lobata*, a similar trend to RMF. RCR and RMF differed significantly at different light intensities.
ties but were not significantly different between the two species. The magnitudes of RCR and RMF were greater in A. artemisiifolia at 30% irradiance, but lower than values for U. lobata at the other three irradiance levels.

RGR and NAR for A. artemisiifolia and U. lobata followed the same pattern as total biomass and leaf area in response to different light intensities. The two traits were strongly affected by irradiance conditions and also varied widely between species. For instance, the RGR and NAR of A. artemisiifolia under full sunlight were about 4.5 and 8.2 times higher than under deep shade. In contrast, light conditions had a relatively smaller effect on RGR and NAR of the native U. lobata, in which RGR and NAR under full sunlight were about 1.8 and 4 times higher than under deep shade. The magnitudes of RGR and NAR of A. artemisiifolia were consistently and significantly higher than for U. lobata under the 30%–100% irradiance levels but lower for U. lobata under deep shade. At this light intensity, RGR and NAR values for A. artemisiifolia fell below those for U. lobata by 45.6% and 36.3%, respectively.

Photosynthetic responses of species to irradiance

Photosynthetic rates of both A. artemisiifolia and U. lobata increased with increasing PPFD until saturation at all levels of irradiance. *Ambrosia artemisiifolia* growing under 100%, 55%, and most of the 30% irradiance conditions (PPFD above 1000 μmol·m⁻²·s⁻¹) generally had higher photosynthetic rates than *U. lobata*, whereas under 10% irradiance, it had lower photosynthetic rates than *U. lobata*.

Light-response curves differed between light environments in the same way for A. artemisiifolia and U. lobata. Leaves of
both species produced under shade conditions had significantly lower photosynthetic rates than leaves produced under high light conditions, though leaf saturation occurred at almost the same PPFDs. The mean estimate of light-saturated photosynthetic rate ($P_{\text{max}}$) differed between the species in that $A. \text{artemisiifolia}$ had significantly higher light-saturated photosynthetic rates than $U. \text{lobata}$ at the 55% and 100% irradiance levels but not at the lower irradiance levels because $P_{\text{max}}$ of $A. \text{artemisiifolia}$ at the 10% irradiance level was 17.2% lower than that of $U. \text{lobata}$ (Fig. 2). The maximum light-saturated photosynthetic rate occurred in full sunlight for both species, with a $P_{\text{max}}$ of $A. \text{artemisiifolia}$ (20.0 μmol·m$^{-2}$·s$^{-1}$) significantly higher than the $P_{\text{max}}$ of $U. \text{lobata}$ (16.5 μmol·m$^{-2}$·s$^{-1}$).

With decreasing irradiance, both species showed remarkable decreases in light saturation (LSPT) and light compensation (LCPT) points and lower rates of dark respiration. The LCPT of $A. \text{artemisiifolia}$ ranged from 22.0 to 39.0 μmol·m$^{-2}$·s$^{-1}$ across the four irradiance levels and was significantly higher for $U. \text{lobata}$ under the same irradiance conditions. $Ambrosia \text{artemisiifolia}$ exhibited significantly lower LSPT (634 μmol·m$^{-2}$·s$^{-1}$) only at the 10% irradiance level, although it tended to be significantly higher than the LSPT of $U. \text{lobata}$ at the other three irradiance levels. Dark respiration rates of $A. \text{artemisiifolia}$ significantly exceeded those of $U. \text{lobata}$ across the different light conditions, except the 10% irradiance level (Fig. 2).

A positive linear relationship between $P_{\text{max}}$ and $R_d$ was detected based on data across all four irradiance treatments. The $P_{\text{max}}$ per unit $R_d$ was higher for $A. \text{artemisiifolia}$ relative to $U. \text{lobata}$ at the 30%–100% irradiance level but was lower at the 10% irradiance level. The slope and intercept of the relationship between $P_{\text{max}}$ and $R_d$ were not significantly different between the two species (Fig. 3).

Relationship among traits

The magnitude of RGR for $A. \text{artemisiifolia}$ and $U. \text{lobata}$ showed a decreasing trend with increasing irradiance level. $Ambrosia \text{artemisiifolia}$ had a relatively higher RGR under a given SLA at irradiances above 10%, whereas it had a lower RGR to variations of SLA below the 10% irradiance level. $Ambrosia \text{artemisiifolia}$ and $U. \text{lobata}$ exhibited the same
general trend in that both LAR and LA:RM increased with the increasing SLA, and the substantial changes of LA:RM occurred at higher range values of SLA, especially in *Ambrosia artemisiifolia*. The responses of LAR to SLA were nearly linear, with the LAR per unit SLA consistently higher for *Ambrosia artemisiifolia* than *Urena lobata*. *Ambrosia artemisiifolia* exhibited lower responses of LAR to variations of SLA than *Urena lobata* (Fig. 3). For both species, NAR was positively related to $P_{\text{max}}$, with *Ambrosia artemisiifolia* having a distinctly higher NAR response to light under all irradiance treatments. RGR of *Ambrosia artemisiifolia* and *Urena lobata* increased with increasing leaf area and $P_{\text{max}}$. Although RGR and LA for both studied species could be expressed by logarithmic curve with the coefficient of determination ($R^2$) as high as 0.99, the slopes of the two regression lines differed, with *Ambrosia artemisiifolia* showing a significantly higher slope than *Urena lobata*. The relationship between RGR and $P_{\text{max}}$ for the two species could be described by an S-shaped curve. For a given $P_{\text{max}}$, RGR values

![Fig. 3. Graphs showing relationships between specific leaf area (SLA) and relative growth rate (RGR), specific leaf area (SLA) and leaf area ratio (LAR), specific leaf area (SLA) and ratio of leaf area to root mass (LA:RM), and light-saturated photosynthetic rate ($P_{\text{max}}$) and net assimilation rate (NAR).](image-url)
for the invasive *A. artemisiifolia* were higher than values for the native *U. lobata* (Fig. 3).

Mean plasticity values of morphological, allocation, and growth traits for *A. artemisiifolia* were 0.62, 0.64, and 0.83, respectively, showing a relatively higher plasticity in morphological structure traits than *U. lobata* (Tables 1 and 2). *Ambrosia artemisiifolia* exhibited a higher plasticity (0.60) of photosynthetic physiologically relevant variables compared with *U. lobata* (0.56). Mean morphological structure and physiological plasticity in response to irradiance did not result in pronounced differences between *A. artemisiifolia* and *U. lobata* (Mann–Whitney *U* test, *p* = 0.213 and 0.564, respectively), though differences in plasticity for various traits were detected. *Ambrosia artemisiifolia* had 27.8%–66.4% greater response to irradiance variation in terms of plant height, leaf area, number of internodes, crown width and area, RGR, and *P* max than *U. lobata*. However, it exhibited lower plasticity indices for LAR, LMA, SLA, SRM, *R* d, and LCPT, especially SLA, for which the plasticity index was nearly 76% lower than that of *U. lobata*.

For both *A. artemisiifolia* and *U. lobata*, plasticity indices were greater for morphological, allocation, and growth traits than for photosynthetic physiological variables, although differences were not significant (for *A. artemisiifolia*, median for morphological structure parameters = 0.69, median for photosynthetic physiological parameters = 0.63, Mann–Whitney *U* test, *p* = 0.604; for *U. lobata*, median for morphological structure parameters = 0.57, median for photosynthetic physiological parameters = 0.48, Mann–Whitney *U* test, *p* = 0.941). Interspecific variations in plasticity indices were greater for morphological structure variables by contrast. The largest differences among species were found for morphological structure variables such as SLA, plant height, and LMA.

**Discussion**

**Specific and total leaf area**

SLA is an important plant trait relative to the regulation and control of plant functions such as carbon assimilation and carbon allocation (*Reich et al. 1997; Lambers and Poorter 2004*). Invasive plants are reported to have leaves with a high SLA with which to produce larger assimilatory surfaces for a given amount of carbon fixed (Baruch and Goldstein 1999). Our data showed that SLA was greater for the exotic annual *A. artemisiifolia* than for the native *U. lobata* except at the 10% irradiance level, which translates to *A. artemisiifolia* having 0.8%–30% more leaf area for every gram of carbon allocated to foliage. This finding is consistent with previous research in which the SLA of exotic plants was found to be higher than co-occurring native plants (*Lake and Leishman 2004; Schumacher et al. 2009*). *Ambrosia artemisiifolia* also exhibited a greater leaf area than *U. lobata* when subjected to different irradiance levels above 10%, which likely increases interception of light and acquisition of CO₂. The combination of increased specific and total leaf area, which generally results in increased light absorption and shading of other species, may be light utilization strategies that increase the competitive ability of *A. artemisiifolia* in high light environments. High SLA, however, may also aid plants to tolerate adverse growing conditions (*Allred et al. 2010*). Deep shade in this study induced increases in SLA, which may sustain growth and carbon acquisition by increasing light-capture efficiency. Despite an inferior response to light in modifying SLA, the relatively higher leaf physiological responses observed for *A. artemisiifolia* may allow this species to tolerate low light conditions.

**Growth rate, leaf area ratio, and light-saturated photosynthetic rate**

RGR is important for securing available resources (*Poorter and Remkes 1990; Grotkopp and Rejmánek 2007*). In general, exotic invasive plants have higher RGR than co-occurring native species (*Burns and Winn 2006; Grotkopp and Rejmánek 2007*). In this study, the exotic invasive *A. artemisiifolia* also exhibited a higher RGR than the native co-occurring *U. lobata*, except at the 10% irradiance level. This finding suggests that invasive species do not have consistently higher RGR than native species across variable environments (*Yamashita et al. 2000*).

RGR is often considered a function of *P* max and LAR (*Kitajima 1994*). In this study, the RGR of *A. artemisiifolia* in full sunlight and at the 55% irradiance level was, on average, 1.3-fold higher than for *U. lobata*. Because *A. artemisiifolia* growing at these two irradiance levels did not differ significantly from *U. lobata* in LAR (Fig. 1E), the higher RGR of *A. artemisiifolia* at these levels is likely attributable to its greater *P* max, which was also about 1.3-fold higher than for *U. lobata*. In contrast, the RGR of *A. artemisiifolia* in deep shade was only half as large as that of *U. lobata*. The significant reduction in RGR was more likely due to its substantially decreased LAR because *P* max of *A. artemisiifolia* and *U. lobata* were nearly equal, whereas LAR of *A. artemisiifolia* was more than 35% less than for *U. lobata*. These results were neither absolutely consistent with some reports in which LAR was demonstrated to be the main factor explaining the variation in RGR among different tree and herbaceous species (*Poorter and Remkes 1990*) nor consistent with reports that greater *P* max was largely responsible for higher RGR of invasive species (*Pattison et al. 1998*). The comparatively lower LAR of invasive *A. artemisiifolia* than the native *U. lobata* may be a response to reductions of whole-plant carbon gains in low light environments (*Givnish 1988*).

**Biomass allocation**

Plant growth is directly influenced by the allocation of biomass between leaves and stems (*Reich et al. 1998*). Our results showed that *A. artemisiifolia* modified biomass allocation in response to different irradiance environments in that it significantly increased biomass allocation to stems and decreased that to roots at lower irradiance levels. By increasing investment in support structures, *A. artemisiifolia* likely enhanced its growth under shade, whereas *U. lobata* allocated a comparatively higher percentage of biomass to leaves, as well as a proportion of biomass to stems for greater structural support. As demonstrated by *Feng et al. (2007a)*, the increased SMF could increase seed production at high-irradiance levels because the apical bud of each branch would differentiate into a flower bud that would eventually produce seeds. A significantly higher SMF for *A. artemisiifolia* relative to *U. lobata* may afford it a competitive advantage and enhance its invasiveness.

Both *A. artemisiifolia* and *U. lobata* showed significantly greater RSRs under high irradiance conditions than in deep shade, which may balance the demands of water and light.
energy capture (Tilman 1988). However, the two species did not differ in RSR nor did they differ in RMF. This finding differed from trends of the other aboveground traits and is consistent with work by Grime (1994) showing that below- and above-ground plant components are interdependent.

**Photosynthetic performance**

Plants growing or acclimated to low light levels tend to have lower photosynthetic capacity, lower light compensation points, and lower dark respiration rates than plants growing under high light conditions (Björkman et al. 1972). In our study, the photosynthetic rates at light saturation, LCPT, and Rg were higher for plants growing under higher irradiance than under shaded conditions for both target species. The LCPT and Rg of *Ambrosia artemisiifolia* were comparatively greater than those of *U. lobata* across the four irradiance regimes. Low LCPTs are demonstrated to be advantageous for plants growing under low-light environments because they possibly aid in maintaining a positive carbon balance (Boardman 1977). Significantly lower LCPTs of *U. lobata* at lower irradiance levels likely afforded it a distinct advantage over *Ambrosia artemisiifolia* in heavily shaded environments such as forest understoreys. Variations of LCPT for invasive *Ambrosia artemisiifolia* and native *U. lobata* are not consistent with other studies showing that native species have higher LCPTs in high light and partial shade conditions (Pattison et al. 1998).

In this study, *Ambrosia artemisiifolia* had significantly higher Pmax than *U. lobata* when growing under high irradiance conditions, confirming that increasing photosynthesis in high light could facilitate its invasive success. *Ambrosia artemisiifolia* had greater LSPT, Pmax, and higher RGR and SLA than *U. lobata*, except at the 10% irradiance level. This invasive plant also exhibited higher photosynthetic capacity under high irradiance conditions (above 10% irradiance) than *U. lobata* (Fig. 3), which may probably be ascribed to its high LSPT and Pmax (Zhao and Chen 2011). High LSPT and Pmax are considered advantageous features for invasive species (Baker 1974; Zheng et al. 2009). Therefore, *Ambrosia artemisiifolia* was more efficient in utilizing light under high irradiance conditions. The range of LSPT and Pmax values for *Ambrosia artemisiifolia* suggests that this invasive species has a greater capacity to modify its photosynthetic response while acclimating to variable light environments. This high physiological plasticity is likely to increase its competitive ability in heterogeneous light conditions.

**Acclimation to light environment**

Both the invader *Ambrosia artemisiifolia* and the native *U. lobata* can grow well under variable light conditions. However, the two species differed in their ability to acclimate to different irradiance levels. *Ambrosia artemisiifolia* survived in the deep shade imposed in this study. In *Ambrosia artemisiifolia*, certain plastic responses suggest great invasion potential. That is, *Ambrosia artemisiifolia* adjusted biomass allocation and SLA and consequently maintained the lowest RMF and RSR and highest leaf, stem biomass, and SLA under the low light treatments. Furthermore, this species maintained a considerable photosynthetic capacity and growth rate in deep shade, suggesting that it has an ability to effectively capture and utilize light in low light environments. Although relatively high phenotypic plasticity under varying irradiance regimes may contribute to *Ambrosia artemisiifolia* invasion, there is no direct relationship between plasticity and invasibility. *Ambrosia artemisiifolia* performed relatively poorly under the lowest light condition compared with the performance of *U. lobata*. This finding is not surprising given that *Ambrosia artemisiifolia* is often limited to highly disturbed, high light environments such as annual cropping systems, roadsides, and vacant lots (Bassett and Crompton 1975; Cole et al. 1981; DiTommaso 2004) where it grows rapidly and intercepts sunlight, thus reducing productivity of other plants. These findings are also consistent with agronomic reports showing that *Ambrosia artemisiifolia* grows as well as sweet corn (*Zea mays* L.) or dry beans (*Vicia* spp.) in 30% shade but grows relatively poorer with these crops in higher (73%) shade (Dickerson 1968; Bassett and Crompton 1975).

Both species performed best in the high irradiance treatments, consistent with their preference for high light habitats. *Ambrosia artemisiifolia* exhibited greater growth and photosynthetic efficiency at intermediate and high light levels. Leaf area and Pmax are two important factors contributing to the higher growth rate of *Ambrosia artemisiifolia*. Greater LMF, total leaf area, and SLA may, in part, allow *Ambrosia artemisiifolia* to aggressively colonize and invade high light environments. The ability of *Ambrosia artemisiifolia* to tolerate heavy shade conditions while exhibiting high growth rates in high light environments is consistent with the response to varying light environments of other invasive species such as common rhododendron (*Rhododendron ponticum* L.) (Niinemets et al. 2003), crofton weed (*Ageratina adenophora* (Spreng.) King & H. Rob.), and bitter bush (*Chromolaena odorata* (L.) King & H. Rob.) (Feng et al. 2007b).

Comparisons between sympatric invasive and noninvasive species with similar ecological niches are a common approach for determining plant traits associated with invasiveness and for improving understanding of invader success. *Urena lobata*, a commonly co-occurring native plant with the exotic *Ambrosia artemisiifolia* in China, was used as a comparative species in this study. This native shrub is considered invasive in some regions of the world including Florida, Hawaii, Louisiana, Puerto Rico, and the US Virgin Islands (Wang et al. 2009). Both species prefer disturbed, high light environments. Thus, knowledge of how *Ambrosia artemisiifolia* and *U. lobata* respond to varying irradiance conditions may provide insights into the performance of this exotic species compared with, presumably, a well adapted and competitive native species under conditions typical of the invaded habitat. Our findings demonstrate that *Ambrosia artemisiifolia* possesses a suite of traits that favours capture and utilization of light, particularly in high light environments. However, *Ambrosia artemisiifolia* did not generally outperform the native species at the lowest irradiance level, as shown by the lower Pmax, SLA, and RGR values relative to *U. lobata*. Although *U. lobata* is considered invasive in some tropic and subtropical regions of the world, its lower performance at high light levels relative to *Ambrosia artemisiifolia* in this study suggests that *U. lobata* may be at a competitive disadvantage and likely to be displaced by *Ambrosia artemisiifolia* in high light habitats where the two species co-occur such as in southern China. Future research should assess competitive outcomes between these two species at varying light environments under both controlled environment and field conditions.
To conclude, *A. artemisiifolia* exhibited significantly higher total biomass, total leaf area, SLA, RGR, and NAR than the native co-occurring species *U. lobata* under intermediate and full light conditions. With decreasing irradiance, *A. artemisiifolia* decreased biomass investment to roots and leaves but increased allocation to support structures. This species is able to tolerate relatively low light conditions but gains a competitive advantage over the native species by its relatively greater growth rate in high light environments such as old fields and roadways. On average, *A. artemisiifolia* displayed higher plasticity in traits pertaining to biomass partitioning, growth, and morphological features. It also exhibited a greater ability to adjust photosynthetic capacities in response to varying light availabilities. However, the performance of *A. artemisiifolia* declined at lower light levels and was outperformed by the native co-occurring species *U. lobata* in deep shade, suggesting that intact low light habitats such as forest understoreys are at lower risk of invasion by this species in southern China.

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