Comparison of Photosynthetic Characteristics Between Two Invasive Asteraceae Species and Native Species in Liaoning Region (Postprint)

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Abstract

To clarify the relationship between the physiological and ecological traits of alien plants and their strong invasiveness, this study employed in-situ field measurements of gas exchange parameters to analyze the differences in photosynthetic characteristics and leaf traits between the Asteraceae invasive plants Ambrosia artemisiifolia and Ambrosia trifida and their co-occurring native plant Aster tataricus. The results showed that the light saturation points (LSP) of all three plants were above 800 mol · m ^{2} · s ^{1}, with the LSP of the two invasive plants being significantly higher than that of A. tataricus, while their apparent quantum yield (AQY) was significantly lower. The maximum net photosynthetic rate (Pnmax) followed the order: A. artemisiifolia > A. trifida > A. tataricus, with Pnmax of A. artemisiifolia and A. trifida being 151.28% and 82.80% higher than that of A. tataricus, respectively (significant differences). The specific leaf area (SLA), leaf nitrogen content per unit mass (Nmass), leaf phosphorus content per unit mass (Pmass), photosynthetic energy use efficiency (PEUE), and photosynthetic nitrogen use efficiency (PNUE) of the two invasive plants were all significantly higher than those of A. tataricus, while there was no significant difference in leaf construction cost per unit mass (CCmass) among the three species. In summary, the two Asteraceae invasive plants in Liaoning exhibited higher gas exchange parameters and leaf trait indices compared to the native co-occurring species, and there was a close relationship between their photosynthetic and leaf characteristics, manifested as higher photosynthetic trait indices and energy utilization indices such as Pnmax, PNUE, PEUE, and water use efficiency (WUE). This enables invasive plants to capture and utilize environmental resources more efficiently, representing one of the reasons for their successful invasion.

Full Text

Comparison of Gas Exchange Characteristics Between Two Invasive Plants and a Co-occurring Native Plant in Liaoning Province

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Abstract

To clarify the relationship between ecophysiological traits and invasiveness in exotic plants, we conducted field measurements of gas exchange parameters to analyze differences in photosynthetic characteristics and leaf traits between two invasive Asteraceae species—Ambrosia artemisiifolia and A. trifida—and their co-occurring native congener, Aster tataricus. The results showed that all three species had light saturation points (LSP) exceeding 800 mol·m ^{2}·s ^{1}, with both invasive species exhibiting significantly higher LSP and lower apparent quantum yield (AQY) than the native species. The maximum net photosynthetic rate (Pnmax) followed the order: A. artemisiifolia > A. trifida > A. tataricus, with the two invasive species showing 151.28% and 82.80% higher Pnmax than the native species, respectively ($P < 0.05$). Specific leaf area (SLA), leaf nitrogen content per unit mass (Nmass), leaf phosphorus content per unit mass (Pmass), photosynthetic energy use efficiency (PEUE), and photosynthetic nitrogen use efficiency (PNUE) were all significantly higher in the invasive species compared to A. tataricus, though no significant differences were observed in leaf construction cost per unit mass (CCmass) among the three species. In summary, the two Asteraceae invasive species in Liaoning exhibited superior gas exchange characteristics and leaf trait metrics relative to the native species. Their photosynthetic and leaf traits were closely linked, as evidenced by higher Pnmax, PNUE, PEUE, and water use efficiency (WUE). These traits enable invasive plants to capture and utilize environmental resources more effectively, which may contribute to their successful invasion.

Keywords: Asteraceae invasive plants; Gas exchange characteristics; Maximum net photosynthetic rate; Leaf traits; Resource utilization efficiency

Introduction

Biological invasion has emerged as one of the most prominent global environmental issues of the 21st century, posing severe threats to ecosystems, agricultural and forestry economies, and public health in invaded regions [1-3]. Invasive plants typically exhibit rapid growth, strong ecological adaptability, high reproductive capacity, and effective dispersal mechanisms [4], which enable them to outcompete native vegetation. While invaders establish and expand their populations in new regions, not all native plants are equally displaced. Comparative studies of physiological and ecological characteristics between invasive species and dominant native congeners provide valuable insights into invasion mechanisms. Beyond growth rate, key indicators associated with competitive ability in invasive plants include high photosynthetic rates, low construction costs (CC), and large total leaf area [5].

Specific leaf area (SLA) serves as an indirect indicator of leaf construction cost [5-6]. Lower construction costs (i.e., higher SLA) imply greater efficiency in utilizing plant carbon assimilation products and higher photosynthetic nitrogen-use efficiency (PNUE) [7-8], which facilitates rapid growth [6] and confers competitive advantages to invaders [9-10]. For instance, Baruch and Goldstein [11] compared 30 invasive and 34 native species in Hawaii, finding that invaders generally had higher SLA and assimilation rates but lower leaf construction costs. Alpert et al. [12] and Wang et al. [13] advocated for comparative studies between closely related invasive and native species (e.g., within the same family or genus). Wang et al. [14] reported that the invasive plant Chromolaena odorata and its native congener Gynura japonica exhibited distinct light adaptation strategies, with the invader showing higher light use efficiency. Similarly, Wang et al. [15] found that the invasive Conyza canadensis had higher photosynthetic rates and biomass accumulation capacity than its associated native species, suggesting that high productivity is a key factor for successful invasion.

In China, the most common invasive plants belong to Asteraceae, Poaceae, and Brassicaceae [1], with Asteraceae representing one of the most speciose invasive groups [16]. Ambrosia artemisiifolia, an annual noxious weed native to North America, is a globally recognized invasive species within the Asteraceae tribe Heliantheae [17]. Its pollen is a potent allergen and major cause of hay fever, posing significant health risks [18]. Ambrosia trifida, also a North American annual weed, was introduced to northeastern China in the 1940s and has become one of the most destructive invasive weeds in northern China [19]. This species forms monospecific stands, causing crop yield losses and threatening biodiversity, while also triggering hay fever in susceptible populations [20-21].

Currently, few studies have compared ecophysiological traits between invasive and non-invasive plants within specific taxonomic groups (family or genus). Since congeners share evolutionary backgrounds and biological characteristics, such comparisons are particularly valuable for elucidating the unique physiological mechanisms underlying invasion success. Therefore, this study compared photosynthetic characteristics and leaf traits between invasive Asteraceae species and native sympatric congeners to explore their response mechanisms to varying light intensities and provide a scientific basis for risk assessment and management of potential invaders.

1.1 Study Area Description

The study site was located at Qipanshan, Shenyang, Liaoning Province (42°1 58 N, 123°51 43 E, elevation 192 m), a heavily infested area with both A. artemisiifolia and A. trifida. The region has a mid-temperate continental monsoon climate with cold, snowy winters and short, hot, rainy summers. The annual mean temperature is 7.41 °C, frost-free period is 148 days, mean annual precipitation is 750 mm, and relative humidity ranges from 65% to 70%. The sampling area represented a typical co-occurrence zone of the two invasive Asteraceae species, characterized by a naturally mixed community of invasive and native plants with patchy distributions of invaders. The native Aster tataricus served as the dominant non-invasive congener, accompanied by other weeds including Humulus scandens, Lactuca indica, and Setaria viridis. Soil type was brown earth with pH 6.4, organic matter 14.62 g · kg ^{1}, total nitrogen 1.53 g · kg ^{1}, and total phosphorus 0.99 g · kg ^{1}.

Measurements and sample collections were conducted on August 27, 2015, when both invasive and native species had completed leaf morphogenesis and were in the peak vegetative growth to early flowering stage.

1.2 Experimental Methods

For each plant species, one experimental block (10 m × 10 m) was established. Within each block, five 1 m × 1 m quadrats were randomly placed. Ten representative plants with relatively uniform growth were selected from each quadrat, and 30 healthy, intact mature leaves were randomly collected from each plant, yielding 5 × 30 = 150 leaves per species. All collections were replicated five times within each quadrat. Leaf area was measured using a Li-3100A leaf area meter (Li-Cor, Lincoln, Nebraska, USA). Leaves were then placed in sealed bags, stored in ice boxes, and transported to the laboratory for determination of chlorophyll content, leaf N and P concentrations, and other physicochemical indicators. Concurrently, soil samples (0–10 cm depth) were collected from the rhizosphere of each plant for physicochemical analysis.

Photosynthesis-light response (Pn-PAR) measurements: Between 9:00–

11:00 AM, plants in the vegetative growth stage were selected from each quadrat. A LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) was used to measure net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs) on functional leaves [22]. Chamber temperature was set at 25 °C, CO concentration at 400 mol · mol ^{1}, and photosynthetically active radiation (PAR) gradients at 2000, 1500, 1000, 800, 500, 300, 100, 50, and 0 mol · m ^{2} · s ^{1} using an automatic measurement program [23]. Fully expanded mature leaves were measured at their natural growth angles, with three measurements per leaf and five replicates per block.

Photosynthetic light-response curves were fitted using the modified rectangular hyperbola model proposed by Ye [24] and Ye et al. [25]:

$$P_n = \frac{\alpha I + P_{nmax} - \sqrt{(\alpha I + P_{nmax})^2 - 4\alpha\gamma I P_{nmax}}}{2\gamma} - R_d$$

where P_n is net photosynthetic rate (mol · m ^{2} · s ^{1}), I is photosynthetically active radiation (mol · m ^{2} · s ^{1}), α is apparent quantum yield (AQY) representing the initial slope of the light-response curve at $I = 0$, β and γ are coefficients independent of I (m^{2} · s · mol ^{1}), and R_d is dark respiration rate (mg · h ^{1} · g ^{1}).

Water use efficiency (WUE) was calculated as [26]:

$$WUE = \frac{P_n}{T_r}$$

where P_n is photosynthetic rate (mol · m ^{2} · s ^{1}) and T_r is transpiration rate (mmol · m ^{2} · s ^{1}).

Chlorophyll content determination: Fresh leaves were cleaned with deionized water. Leaf discs were cut with a punch, sliced into thin strips, and extracted with 80% acetone until completely bleached. Optical density was read at 663 nm and 645 nm (denoted as OD   and OD   ), and chlorophyll content was calculated as [27]:

$$\rho(Chla) = 12.7 \times OD_{663} - 2.69 \times OD_{645}$$

$$\rho(Chlb) = 22.9 \times OD_{645} - 4.68 \times OD_{663}$$

$$\rho(Chl) = \rho(Chla) + \rho(Chlb)$$

where $\rho(Chla)$ and $\rho(Chlb)$ are chlorophyll a and b concentrations (mg · L ^{1}), and $\rho(Chl)$ is total chlorophyll concentration (mg · L ^{1}).

Leaf element content analysis: Plant samples were oven-dried at 105 °C for 30 min, then at 65 °C to constant weight. Dried leaves were ground, sieved, and stored in sealed bags. Total N was determined by Kjeldahl digestion, and total P by molybdenum-antimony colorimetry [28-30].

Leaf ash content and construction cost: Samples were combusted in a muffle furnace at 500 °C for 6 h, and the remaining residue was weighed. Dry weight calorific value was measured using an oxygen bomb calorimeter (HWR-15E, Shanghai Shangli Testing Instrument Factory). Approximately 0.5 g of powdered plant material was completely combusted, with five replicates per sample averaged to obtain the dry weight calorific value [31].

Leaf construction cost per unit mass (CCmass) was calculated as [31-32]:

$$CC_{mass} = \frac{0.06968 \times (CV \times \frac{100-Ash}{100} + 5.325 \times ON \times EG)}{k}$$

where CV is dry weight calorific value ($\mathrm{kJ \cdot g}^{\ 1}$), Ash is ash content (%), ON is organic nitrogen content (%), EG is growth efficiency, and k is the oxidation state of nitrogen. The average leaf growth efficiency for different plants is 0.87 [33]. For each sample, calculations were performed separately using both ammonium nitrogen (-3 oxidation state) and nitrate nitrogen (+5 oxidation state), then weighted according to the ratio of NH -N to NO -N in the soil to obtain the final CCmass.

Additional calculations:

$$SLA = \frac{ULA}{DW}$$

$$CC_{area} = \frac{CC_{mass}}{SLA}$$

$$N_{area} = N_{mass} \times SLA$$

$$PEUE = \frac{P_{nmax}}{CC_{area}}$$

$$PNUE = \frac{P_{nmax}}{N_{area}}$$

where SLA is specific leaf area ($\mathrm{cm}^2 \cdot \mathrm{g}^{\ 1}$), ULA is unit leaf area (cm^2), DW is leaf dry weight (g), CC_{area} is leaf construction cost per unit area [g(glucose) $\cdot$ $\mathrm{m}^{\ 2}$], N_{mass} is leaf N content per unit mass ($\mathrm{mg} \cdot \mathrm{g}^{\ 1}$), N_{area} is leaf N content per unit area ($\mathrm{g} \cdot \mathrm{m}^{\ 2}$), $PEUE$ is photosynthetic energy use efficiency [μmol(CO) · g ^{1}(glucose) · s ^{1}], and *PNUE* is photosynthetic nitrogen use efficiency [μmol(CO) · g ^{1} · s ^{1}].

1.3 Data Analysis

Light saturation point (LSP), light compensation point (LCP), apparent quantum yield (AQY), and maximum net photosynthetic rate (Pnmax) were calculated following the methods of Chen et al. [23]. All data were analyzed using SPSS 16.0 and plotted with Excel 2007. Results are presented as means ± standard errors. One-way ANOVA and least significant difference (LSD) tests were used for interspecific comparisons at $P = 0.05$.

2.1 Photosynthetic Light Response of Invasive and Native Asteraceae Species

As shown in [Figure 1: see original paper], net photosynthetic rate (Pn) in both invasive species (A. artemisiifolia and A. trifida) and the native species (A. tataricus) initially increased then plateaued with increasing PAR, with the invasive species showing greater increases. At specific PAR levels, Pn reached maximum values corresponding to the light saturation point. The relationships between Pn and PAR were highly significant for all three species (A. artemisiifolia: $R^2 = 0.997$, $P < 0.001$; A. trifida: $R^2 = 0.999$, $P < 0.001$; A. tataricus: $R^2 = 0.995$, $P < 0.001$). Photosynthetic response parameters calculated from the modified rectangular hyperbola model are presented in .

All three species had LSP values exceeding 800 mol · m ^{2} · s ^{1}, following the order: A. trifida > A. artemisiifolia > A. tataricus, with significant differences among them. Light compensation point (LCP) followed the order: A. tataricus > A. trifida > A. artemisiifolia, with the native species showing significantly higher LCP (30.736 mol · m ^{2} · s ^{1}) than A. artemisiifolia. Both invasive species had significantly lower AQY than the native species ($P < 0.05$). Pnmax followed the order: A. artemisiifolia > A. trifida > A. tataricus, with the invasive species showing 151.28% and 82.80% higher values than the native species, respectively ($P < 0.05$). These results demonstrate that the two invasive Asteraceae species have higher light use efficiency and stronger photosynthetic assimilation capacity under equivalent PAR conditions.

Stomatal conductance (Gs), transpiration rate (Tr), and water use efficiency (WUE) increased with PAR in all three species. However, when PAR exceeded 500 mol · m ^{2} · s ^{1}, Gs, Tr, and WUE in the native species plateaued, whereas both invasive species continued to show increases in Gs and Tr. As shown in [Figure 1d: see original paper], the invasive species exhibited substantially greater increases in WUE with increasing PAR compared to the native species, indicating superior water use efficiency.

2.2 Leaf Trait Comparisons Between Invasive and Native Species

As presented in , chlorophyll content was significantly higher in both invasive species than in the native species ($P < 0.05$), following the order: A. artemisiifolia > A. trifida > A. tataricus. Specific leaf area (SLA), leaf nitrogen content per unit mass (Nmass), leaf phosphorus content per unit mass (Pmass), photosynthetic energy use efficiency (PEUE), and photosynthetic nitrogen use efficiency (PNUE) were all significantly higher in the invasive species compared to A. tataricus ($P < 0.05$). However, no significant differences were observed in leaf construction cost per unit mass (CCmass) among the three species.

Discussion

Invasive plants can fundamentally alter the biological characteristics of natural communities [34-35]. Successful invasion depends on multiple factors, among which physiological traits are critical for survival, establishment, and expansion. Some exotic species possess stronger light use efficiency, photosynthetic response mechanisms, and ecophysiological characteristics than native species, conferring high invasion potential [36]. Plant invasiveness is determined by interactions between environmental factors and intrinsic plant traits. Under equivalent reproductive capacity and herbivore pressure, invasive species can rapidly displace native plants, presumably by more efficiently utilizing limited resources or by exploiting resources at times when natives cannot [37].

3.1 Differences in Gas Exchange Parameters Plant light capture capacity and photosynthetic acclimation largely reflect growth and competitive abilities [38]. Light saturation point (LSP) and light compensation point (LCP) indicate adaptability to high and low light conditions [39], while AQY and Pn reflect photosynthetic efficiency and primary productivity [40]. In this study, the invasive species showed greater increases in Pn, Gs, and WUE within certain light ranges compared to the native species, suggesting greater stomatal flexibility and regulatory capacity. This enables invasive plants to assimilate more CO while minimizing water loss under varying environmental conditions.

Water use efficiency is a crucial indicator of plant water physiology, particularly important in arid environments [26]. Despite increased Gs with rising PAR, invasive species maintained high WUE, likely because enhanced Pnmax compensated for water loss [41]. Both invasive species achieved higher maximum WUE values than the native species. These findings align with previous studies showing higher WUE in invasive species such as Ageratina adenophora [42] and Conyza canadensis [15] compared to their native counterparts.

3.2 Differences in Leaf Trait Indicators Since CO assimilation occurs in chloroplasts, chlorophyll content directly affects photosynthesis [44]. Both invasive species had significantly higher chlorophyll content than the native species. Specific leaf area is closely related to nitrogen allocation [45]; high nitrogen promotes photosynthetic capacity and carbon accumulation in invasive plants [46]. Phosphorus plays vital roles in membrane structure, metabolism, enzyme regulation, and signal transduction, and is essential for photosynthesis [47]. Higher leaf N and P contents enhance both plant growth and photosynthetic capacity [45]. The significantly higher Nmass and Pmass in the invasive species suggest stronger nutrient uptake and utilization abilities [37].

Feng et al. [42] proposed that invasive populations may exhibit higher Nmass and SLA than native populations due to evolutionary shifts in resource allocation. With reduced herbivore pressure in introduced ranges, invaders may allocate less nitrogen to defense (cell wall synthesis) and more to photosynthesis, thereby enhancing competitiveness. This study supports this hypothesis, as both invasive species showed significantly higher SLA, Nmass, and Pmass than the native species.

Construction cost (CCmass), PEUE, and PNUE are important indicators of plant energy use strategies [33]. While lower CCmass could confer competitive advantages [32], this study found no significant differences in CCmass among species despite higher Pnmax in invaders. This may be attributed to high nitrogen content and the energy demands of synthesizing proteins and amino acids, which increase CCmass [42]. The significantly higher PNUE and PEUE in invasive species compared to natives [49] indicate more efficient resource acquisition strategies.

Photosynthetic rate (Pn) is the most critical parameter determining biomass accumulation capacity, growth rate, and competitive strength [50]. The higher Pn in A. artemisiifolia and A. trifida did not result in lower CCmass, consistent with findings by Penning de Vries et al. [33] and Feng et al. [42]. This suggests that elevated PEUE and PNUE—key indicators of leaf energy use efficiency [51] —may offset the costs of higher CCmass, making these metrics more relevant for assessing resource acquisition capacity.

In conclusion, this study demonstrates that the net photosynthetic rates of A. artemisiifolia, A. trifida, and A. tataricus are all highly significantly correlated with PAR. All three species have LSP values above 800 $\mathrm{mol} \cdot \mathrm{m}^{2} \cdot \mathrm{s}^{1}$, following the order A. trifida > A. artemisiifolia > A. tataricus. LCP followed the order A. tataricus > A. trifida > A. artemisiifolia, with the native species significantly higher than A. artemisiifolia. Both invasive species had significantly lower AQY but higher Pnmax than the native species. The invasive species also showed greater increases in WUE with increasing PAR. Overall, under identical conditions, the two invasive species demonstrated superior photosynthetic capacity, light use efficiency, and water use efficiency compared to the native species.

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