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

Authors: Wei Zishang, Chen Xinwei, Yang Dianlin, Huangfu Chaohe

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Abstract

To elucidate the relationship between the physio-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 point (LSP) values of the three plants —A. artemisiifolia, A. trifida, and A. tataricus—were all above 800 mol · m 2 · s 1, and the LSP of the two invasive plants was significantly higher than that of A. tataricus, while their apparent quantum yield (AQY) was significantly lower than that of A. tataricus. The maximum net photosynthetic rate (Pnmax) of the three plants followed the order: A. artemisiifolia > A. trifida > A. tataricus, with the Pnmax of A. artemisiifolia and A. trifida being 151.28% and 82.80% higher than that of A. tataricus, respectively, and the differences were significant. 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, but 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 existed a close relationship between their photosynthetic characteristics and leaf traits, manifested in these Asteraceae invasive plants having higher photosynthetic characteristic indices and energy utilization indices such as Pnmax, PNUE, PEUE, and water use efficiency (WUE), enabling the invasive plants to capture and utilize environmental resources more efficiently, which constitutes one of the reasons for their successful invasion.

Full Text

Preamble

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

WEI Zishang[1,2], CHEN Xinwei[1,2], YANG Dianlin[1], HUANGFU Chaohe[1,2]
(1. Agro-Environmental Protection Institute, Ministry of Agriculture, Tianjin 300191, China;
2. College of Plant Protection, Shenyang Agricultural University, Shenyang 110866, China)

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—common ragweed (*Ambrosia artemisiifolia*) and giant ragweed (*Ambrosia trifida*)—and their co-occurring native congener, *Aster tataricus*. The results revealed 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) compared to the native species. Maximum net photosynthetic rate (Pnmax) followed the order: *A. artemisiifolia* > *A. trifida* > *A. tataricus*, with the two invasives 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, though leaf construction cost per unit mass (CCmass) did not differ significantly among the three species. In summary, the two Asteraceae invaders 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 enhanced traits enable invasive plants to capture and utilize environmental resources more effectively, likely contributing to their successful invasion.

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

Introduction

Biological invasion poses one of the most serious environmental challenges of the 21st century, threatening ecosystems, agricultural economies, and public health worldwide [1-3]. Invasive plants typically exhibit rapid growth, strong ecological adaptability, high reproductive capacity, and efficient dispersal mechanisms [4], enabling them to outcompete native vegetation. While not all native species are displaced by invaders, comparative studies of physiological and ecological traits between invasive and co-occurring native species provide valuable insights into invasion mechanisms. Beyond growth rate, key indicators associated with competitive ability 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 assimilates 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 using closely related invasive and native species (e.g., within the same family or genus). Wang et al. [14] reported that *Chromolaena odorata* (Asteraceae) exhibited higher light use efficiency than its native congener *Gynura japonica*. Similarly, Wang et al. [15] found that the invasive plant *Conyza canadensis* had higher photosynthetic rates and biomass accumulation capacity than its associated native species, suggesting that high productivity contributes significantly to invasion success.

In China, the most common invasive plants belong to Asteraceae, Poaceae, and Brassicaceae [1], with Asteraceae representing one of the most heavily invaded families [16]. *Ambrosia artemisiifolia*, a North American annual weed in the tribe Heliantheae, is a globally recognized noxious invader [17] whose pollen is a potent allergen and major cause of hay fever, posing serious public 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 triggering hay fever in susceptible populations [20-21].

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

1. Materials and Methods

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 of both ragweed species. The region has a mid-temperate continental monsoon climate with cold, snowy winters and short, hot, rainy summers. Mean annual 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 where invasive and native plants formed natural mixed communities with patchy distributions of invaders. The native species *Aster tataricus* (Asteraceae) was the dominant non-invasive associate, 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 collection were conducted on August 27, 2015, when both invasive and native Asteraceae 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 10 m × 10 m experimental block 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 $5 \times 30 = 150$ leaves per species. All sampling was 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 indices. 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 automated measurement program [23]. Fully expanded mature leaves were measured while maintaining their natural orientation, with three measurements per leaf and five replicates per quadrat.

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

$$Pn = \frac{\alpha I + Pn_{max} - \sqrt{(\alpha I + Pn_{max})^2 - 4\alpha\beta I Pn_{max}}}{2\beta} - Rd$$

where Pn is net photosynthetic rate (mol•m ^{2}•s ^{1}), I is photosynthetically active radiation (mol • m ^{2} • s ^{1}), is AQY (apparent quantum yield) representing the slope at $I = 0$, and are coefficients independent of I (m^{2} • s • mol ^{1}), and Rd is dark respiration rate (mg • h ^{1} • g ^{1}).

Water Use Efficiency (WUE): Calculated as [26]:

$$WUE = \frac{Pn}{Tr}$$

where Pn is photosynthetic rate (mol • m ^{2} • s ^{1}) and Tr is transpiration rate (mmol • m ^{2} • s ^{1}).

Chlorophyll Content Determination: Fresh leaves were cleaned with deionized water, punched into discs, and cut into thin strips. Pigments were extracted in 80% acetone until the strips turned completely white. Optical density was measured at 663 nm and 645 nm (OD , OD), and chlorophyll content 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 *(Chla)*, *(Chlb)* are chlorophyll a and b concentrations (mg • L ^{1}), and *(Chl)* is total chlorophyll concentration (mg • L ^{1}).

Leaf Element Content Analysis: Plant samples were killed at 105 °C for 30 min, then oven-dried 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 ashed 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 combusted completely, with five replicates per sample averaged to obtain dry weight calorific value [31].

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

$$CC_{mass} = \frac{(0.06968 \times CV - 0.065) \times (1 - Ash) + 7.5 \times k \times ON/14.0067}{EG}$$

where *Hc* is ash-free calorific value (kJ · g ^{1}), *Ash* is ash content (%), *CV* is dry weight calorific value (kJ · g ^{1}), *CCmass* is leaf construction cost per unit mass [g(glucose) · g ^{1}], *ON* is organic nitrogen content (%), *EG* is growth efficiency, and *k* is the oxidation state of nitrogen [31-32]. The average leaf growth efficiency for different plants is 0.87 [33]. For each sample, calculations were performed separately using both ammonium nitrogen (-3 valence) and nitrate nitrogen (+5 valence) as nitrogen oxidation states, then weighted averages were computed based on soil NH -N and NO -N ratios to determine final CCmass.

Additional calculations:

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

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

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

$$PEUE = \frac{Pn_{max}}{CC_{area}}$$

$$PNUE = \frac{Pn_{max}}{N_{area}}$$

where *SLA* is specific leaf area (cm^{2} · g ^{1}), *ULA* is unit leaf area (cm^{2}), *DW* is leaf dry weight (g), *CCarea* is leaf construction cost per unit area [g(glucose) · m ^{2}], *Nmass* is leaf N content per unit mass (mg · g ^{1}), *Narea* is leaf N content per unit area (g · 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 Chen et al. [23]. All data were analyzed using SPSS 16.0 and plotted with Excel 2007. Results are presented as means ± standard error. One-way ANOVA and least significant difference (LSD) tests were used for interspecific comparisons at P = 0.05.

2. Results

2.1 Photosynthetic Response to Photosynthetically Active Radiation

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

All three species had LSP values exceeding 800 $\text{mol} \cdot \text{m}^{2} \cdot \text{s}^{1}$, following the order: *A. trifida* > *A. artemisiifolia* > *A. tataricus*, with significant differences among them. Light compensation point (LCP) ranked as *A. tataricus* > *A. trifida* > *A. artemisiifolia*, with the native species' LCP (30.736 $\text{mol} \cdot \text{m}^{2} \cdot \text{s}^{1}$) significantly higher than that of *A. artemisiifolia*. Both invasive species had significantly lower AQY than the native species ($P < 0.05$). Maximum net photosynthetic rate followed the order: *A. artemisiifolia* > *A. trifida* > *A. tataricus*, with invasive species showing 151.28% and 82.80% higher Pnmax than the native species, respectively ($P < 0.05$). These results demonstrate that the two invasive Asteraceae species possess higher light use efficiency and stronger photosynthetic assimilation capacity under identical 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 $\text{mol} \cdot \text{m}^{2} \cdot \text{s}^{1}$, Gs, Tr, and WUE in the native *A. tataricus* plateaued rather than continuing to increase, whereas both invasive species maintained increasing Gs and Tr. As shown in [Figure 1: see original paper]d, WUE increased more dramatically with PAR in the invasive species compared to the native species, indicating superior water use efficiency.

2.2 Leaf Trait Comparisons

As shown in , chlorophyll content was significantly higher in both invasive species than in the native species ($P < 0.05$), ranking: *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 the native *A. tataricus* ($P < 0.05$). However, leaf construction cost per unit mass (CCmass) did not differ significantly among the three species.

3. Discussion

Invasive plants can fundamentally alter the biological characteristics of natural communities [34-35]. Successful invasion depends on multiple factors, with physiological traits being critical for survival, establishment, and spread. Some exotic species possess stronger light use efficiency, photosynthetic responsiveness, and ecophysiological characteristics than natives, conferring high invasion potential [36]. Plant invasiveness is determined by interactions between environmental factors and plant traits; under equivalent reproductive capacity and enemy pressure, invasive species often outcompete natives by more efficiently utilizing limited resources or exploiting resources at times when natives cannot [37].

3.1 Differences in Gas Exchange Parameters

Plant light absorption capacity and photosynthetic acclimation largely reflect growth and competitive ability [38]. Light saturation point (LSP) and light compensation point (LCP) indicate adaptability to high and low light environments [39], while AQY and Pn reflect photosynthetic apparatus efficiency and primary productivity [40]. In this study, the greater increases in Pn, Gs, and WUE in invasive ragweed species compared to native *A. tataricus* suggest broader stomatal plasticity, enabling invaders to adjust to environmental changes and assimilate more CO with minimal water loss. Water use efficiency is a crucial physiological indicator, particularly important for plants in arid environments [26]. Despite increasing Gs with PAR, invasive species maintained high WUE because enhanced Pnmax compensated for water loss [41]. Both ragweed species achieved higher maximum WUE than the native species, confirming their superior water use efficiency. These findings align with studies on *Ageratina adenophora* [42] and *Conyza canadensis* [15], which also reported higher WUE in invaders compared to co-occurring natives.

3.2 Differences in Leaf Traits

Since CO assimilation occurs in chloroplasts, chlorophyll content directly affects photosynthesis [44]. Both invasive ragweed species had significantly higher chlorophyll content than native *A. tataricus*. SLA is closely related to nitrogen allocation [45]; high nitrogen enhances photosynthetic capacity and carbon accumulation in invasive plants [46]. Phosphorus plays vital roles in membrane structure, metabolism, enzyme regulation, and signal transduction, significantly impacting photosynthesis [47]. Higher leaf N and P contents promote plant growth and photosynthetic capacity [45]. In this study, both invasive species had significantly higher Nmass and Pmass than the native species, suggesting stronger nutrient uptake capabilities [37].

Feng et al. [42] proposed that invasive populations evolve higher Nmass and SLA than native conspecifics due to enemy release. With reduced herbivore pressure in introduced ranges, invaders allocate less nitrogen to cell walls (defense compounds) and more to photosynthetic machinery, enhancing competitiveness. Both ragweed species showed significantly higher SLA than the native species, along with elevated Nmass and Pmass. Construction cost (CCmass), PEUE, and PNUE reflect plant energy strategies [33]. While lower CCmass could confer competitive advantages [32], the high Pnmax in invasive species did not correspond to lower CCmass, likely because high nitrogen content and protein synthesis costs increase construction costs [42], consistent with Geng et al. [41]. PNUE represents nitrogen utilization efficiency [48], while PEUE directly reflects energy use efficiency. Both parameters were significantly higher in invasive species, corroborating Funk et al. [49].

Photosynthetic rate (Pn) determines carbon accumulation capacity and competitive strength [50]. The high Pn in invasive species did not reduce CCmass, consistent with Penning de Vries et al. [33] and Feng et al. [42], likely because elevated PEUE and PNUE—key indicators of leaf energy use efficiency [51]—offset higher construction costs, making these parameters more relevant for assessing resource acquisition capacity.

Conclusion

This study demonstrates that net photosynthetic rates of both invasive ragweed species and native *A. tataricus* are highly significantly correlated with PAR. All three species had LSP values above 800 mol · m^{2} · s^{1}, ranking: *A. trifida* > *A. artemisiifolia* > *A. tataricus*. LCP ranked: *A. tataricus* > *A. trifida* > *A. artemisiifolia*, with the native species significantly higher than *A. artemisiifolia*. Both invasive species had significantly lower AQY than the native species. Pnmax ranked: *A. artemisiifolia* > *A. trifida* > *A. tataricus*. The invasive species showed greater WUE enhancement with increasing PAR. Overall, under identical conditions, the two invasive Asteraceae species demonstrated superior photosynthetic capacity, light use efficiency, and water use efficiency compared to the native species.

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