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Exploring the differences in the invasion potential of *Sphagneticola trilobata* in three invasive habitats based on photosynthetic and photoprotective capacities

Z.C. YU*, H. ZHU*, Y.Z. ZHENG*, S.Y. YU*, Y.F. LIU**, X.L. LIN*, C.L. PENG***, and X.T. ZHENG*,+

*School of Life Sciences and Food Engineering, Hanshan Normal University, 521041 Chaozhou, China**
*School of Chemistry and Environmental Engineering, Hanshan Normal University, 521041 Chaozhou, China***
Guangdong Provincial Key Laboratory of Biotechnology for Plant Development, Guangzhou Key Laboratory
of Subtropical Biodiversity and Biomonitoring, School of Life Sciences, South China Normal University,
*510631 Guangzhou, China****

Abstract

Few studies have simultaneously assessed the growth characteristics and invasion potential of invasive plants in different habitats by integrating photosynthetic physiology with photoprotective strategies. In this study, we compared the growth, photosynthetic physiology, and photoprotective strategies of the widespread invasive plant *Sphagneticola trilobata* in three representative habitats: farmland, woodland, and riverside. Our results showed that *S. trilobata* exhibited the highest growth performance in farmland, which correlated with the highest net photosynthetic rate, electron transfer rate, and antioxidant substances. Plants from the riverside habitat showed intermediate growth, with the highest quantum yield of unregulated energy dissipation at PSII. Plants in the woodland had the worst growth status. These findings suggest that *S. trilobata* possesses the strongest invasion potential in farmland, intermediate potential at the riverside, and the weakest in woodland. This study provides novel insights for habitat-specific invasion risk assessment of alien plant species.

Keywords: adaptation; invasive habitats; invasive plants; photoprotective capacity; photosynthetic capacity; *Sphagneticola trilobata*; tolerance.

Introduction

The rapid advancement of globalization is a significant driver of biological invasions (Fuentes *et al.* 2015, van Kleunen *et al.* 2020). Currently, biological invasions have become a significant biosecurity issue worldwide, posing a substantial threat to global biodiversity, economic development, and ecosystem function (Rejmánek 2015, van Kleunen *et al.* 2015). To achieve successful establishment in new habitats, invasive alien organisms

Highlights

- *S. trilobata* employs differentiated adaptation strategies in different habitats
- The synergism of photoprotection and photosynthesis is key to successful invasion
- Flexible photoprotection capacity gives invasive plants greater tolerance

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+Corresponding author
e-mail: 1354424534@qq.com

Abbreviations: BW – bound water content; Car/Chl – carotenoids to total chlorophyll ratio; Chl – chlorophyll; DSSN – diameter of second stem node; ETR – electron transfer rate; Fla – flavonoids; F_v/F_m – maximum quantum yield of PSII photochemistry; FW – free water content; FW/BW – ratio of free water to bound water; IPM – individual plant mass; LDMC – leaf dry matter content; LIP – length of individual plant; LMA – leaf mass per area; LSSN – length of second stem node; LT – leaf thickness; LTSN – length of third stem node; Phe – phenolics; P_N – maximum net photosynthetic rate; SLA – specific leaf area; TAC – total antioxidant capacity; $Y_{(II)}$ – actual photochemical efficiency of PSII; $Y_{(NO)}$ – the quantum yield of unregulated energy dissipation at PSII; $Y_{(NPQ)}$ – quantum yield of regulatory energy dissipation at PSII.

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often undergo various adaptive evolutionary changes (Colautti and Lau 2015). Studies have shown that several functional traits appear to enhance the invasiveness of alien plants (van Kleunen *et al*. 2010). To adapt to varying environmental conditions within the introduced range, these plants commonly alter traits associated with invasiveness, such as increased relative growth rates (Godoy *et al*. 2011), lower leaf mass per unit area (Molina-Montenegro *et al.* 2013), and higher photosynthetic rates (Funk and Vitousek 2007, Molina-Montenegro *et al.* 2010). These adjustments reflect a strategy of efficient exploitation and utilization of environmental resources by invasive plants (Matzek 2011). At the same time, applications based on the nutritional and functional potential of such plants are rapidly developing. Current research focuses on regulating plant responses to environmental stress and exploring ways to enhance their biochemical and physiological properties (Martínez-Chávez *et al.* 2024, Sytar *et al.* 2025). Different functional traits can lead to distinct resource utilization strategies in invasive plants. Thus, by modulating the combination of relevant traits, invasive plants can increase their capacity to exploit local resources, thereby facilitating a more successful invasion.

Previous studies have shown that the distribution of plant functional traits may be closely related to environmental factors (Butler *et al.* 2017, Blonder *et al.* 2018, Boonman *et al*. 2020, Kanta *et al*. 2024, Asao *et al.* 2025). Functional traits contribute to plant invasion and can significantly influence habitat adaptation (Kunstler *et al.* 2016, Carboni *et al.* 2018). Scholars note that invasive plants often show considerable trait variation across habitats. Differences in functional traits and their plasticity may help invasive plants mediate the limited availability of resources, thereby affecting their invasion potential in different environments, which is closely related to resource utilization and competition (Carboni *et al.* 2018). For example, in order to gain a higher competitive advantage, invasive plants may exhibit greater phenotypic plasticity in traits that allow them to survive the invasion process and spread to other regions (Blonder *et al*. 2018). In resource-poor habitats, they can adjust physiological or morphological traits to mitigate the effects of spatial variations in light and temporal variations in water and nutrients (Davis *et al.* 2000). Under constraints such as limited water, light, or nutrients, invasive plants often exhibit enhanced transient resource-use efficiency (Funk and Vitousek 2007). In addition, invasive plants have demonstrated superior adaptability under various types of environmental stresses. Under high-temperature and high-light conditions, the invasive plant *Sphagneticola trilobata* mitigates the damage to the photosynthetic system caused by excess light energy by increasing the proportion of xanthophyll-dependent thermal dissipation and constitutive thermal dissipation (Song *et al.* 2010). It also increases the content of antioxidant substances and the activity of antioxidant enzymes to resist high-temperature stress (Cai *et al.* 2021b). In response to nitrogen deposition, low temperature, low light, or cadmium stress, invasive plants show enhanced tolerance through physiological adjustments, such as changes in photosynthetic rate, specific leaf area (SLA), and nutrient uptake (Sun *et al.* 2015, Zhang *et al.* 2020). A warming climate will increase the biomass of invasive plants (Lin *et al.* 2010). Invasive plants also show favorable growth under drought conditions (Zhang *et al*. 2021). In summary, these studies illustrate how invasive plants adapt to environmental changes through diverse mechanisms, facilitating their range expansion. This adaptability may explain their rapid evolution and successful invasion across varied environments (Colautti and Barrett 2013, van Boheemen *et al*. 2019).

Abiotic environmental factors in different habitats often show a spatially heterogeneous distribution (Peipoch *et al.* 2016). During invasion, plants may encounter variations in light, soil nutrients, or water availability. To adapt to such environmental changes, they can adjust their physiological functions, thereby enhancing their ability to utilize heterogeneous resources and strengthening their invasion potential (Wang *et al*. 2008). Interestingly, although invasive plants may show unexpected success in a variety of environments, they do not always exhibit equal growth advantages across all habitats. This is because their physiological responses can vary significantly depending on the habitat (Scasta *et al*. 2016). Accordingly, the physiological traits, functional traits, and biomass of invasive plants may also differ in response to environmental heterogeneity. Therefore, clarifying how invasive plants respond to environmental changes across habitats helps uncover the mechanisms behind their success in invasion and is crucial for designing effective management and prevention strategies. However, few studies have explored differences in the potential invasive capacity of invasive plants across different habitats in terms of photosynthetic and photoprotective physiology. This study focuses on *S. trilobata*. Native to South and Central America, its original distribution ranges from Mexico and the Caribbean to Brazil (Zhang *et al*. 2024a,b; Kato-Noguchi and Kato 2025). Initially introduced as an ornamental plant in many countries, it escaped cultivation and became a highly damaging invasive species in the wild. Currently, *S. trilobata* has invaded many tropical and subtropical regions worldwide (Kato-Noguchi and Kato 2025). Given that the climate of southern China resembles its native tropical habitat, and given its strong ecological adaptability and stress tolerance, it has become a common invasive plant in this region (Cai *et al.* 2021a,b; 2024; Zhang *et al*. 2021, 2024a,b). In this study, we conducted a series of physiological and biochemical experiments on *S. trilobata* from different habitats. We compared plant growth, photosynthetic capacity, leaf functional traits, chlorophyll fluorescence, and photoprotective ability across habitats. Furthermore, we examined how photosynthetic physiology and photoprotective responses vary under different environmental conditions. Finally, by integrating biomass data, we evaluated which habitat confers a greater invasion potential for *S. trilobata*. This work provides a theoretical basis for predicting the spatial distribution of invasive plants and assessing invasion risks across different habitats.

Materials and methods

Plant material: The experimental site of this study was located in Chaozhou City, Guangdong Province, China (N 23°45', E 116°36'). This region experiences a subtropical monsoon climate, characterized by an average annual radiation of 4,665 MJ m^{-2} a^{-1}, a mean annual sunshine duration of 1,433 h, an average annual temperature of 21°C, and an average annual rainfall of 1,700 mm. There are distinct dry and wet seasons throughout the year, with rainfall predominantly concentrated in the wet season from April to September. In this study, we investigated the common invasive plant, *S. trilobata*, across three of its typical habitats of invasion: farmland, woodland, and riverside. The selected sites within each habitat shared similar natural conditions, including elevation, landform, slope, and soil type. For each habitat type, three distinct sampling zones were established, spaced 8–10 km apart, where the invasive population had been established for 3–5 years. All selected areas were characterized by a dense *S. trilobata* population, covering 70–100% of the ground surface. Fieldwork was conducted from June 2023 to August 2024. For analysis, we collected mature, fully expanded leaves from the third stem node of *S. trilobata* plants in each habitat. These samples were used to measure various functional, physiological, and biochemical traits, with a minimum of five biological replicates per trait. Furthermore, we measured several growth parameters on healthy plants during the experimental period: plant height (defined as the vertical extension from ground level), the fresh mass of a single genet (obtained by tracing the main root and stem and collecting all connected ramets for weighing), and the length and diameter of the second and third stem internodes.

Morphological traits of leaves: In each habitat, five well-grown individuals were randomly selected. From each plant, leaves from the second and third stem nodes were collected, rinsed with distilled water, and gently blotted dry. The fresh mass of these leaves was immediately measured. Next, the leaves were placed on a white sheet of paper with a prearranged scale and photographed using a camera. The images were then imported into the *ImageJ* software to analyze leaf area. After imaging, the leaves were dried in an oven at 40°C for 4 h, followed by drying at 75°C for 72 h. The dry masses (DW1 and DW2) were recorded after each step. Finally, the following parameters were calculated for each leaf sample: the free water content (FW), bound water content (BW), ratio of free water to bound water (FW/BW), leaf dry matter content (LDMC), leaf mass per area (LMA), specific leaf area (SLA), and leaf thickness (LT).

Photosynthetic pigment content: Using a 6-mm diameter hole punch, we collected two leaf discs from areas avoiding the main veins. These discs were then cut into smaller pieces using scissors and transferred into a 2-mL centrifuge tube. Next, 1.5 mL of 80% acetone was added and placed in the dark at 4°C for 24 h. During this period, the tubes were shaken gently every 8 h. When the leaf tissue became colorless, the extraction of photosynthetic pigments was considered complete. Absorbance was measured at 663, 645, and 470 nm using a *UV-2450* spectrophotometer (*Shimadzu*, Tokyo, Japan), with 80% acetone as the blank. The photosynthetic pigment content was calculated using the formula of Wellburn (1994). Five biological replicates were performed for samples from each habitat.

Flavonoid content: The determination of flavonoid content was based on the method of Heimler *et al*. (2005) with appropriate modifications. Two leaf discs were harvested using a 6-mm diameter punch from interveinal regions and transferred to a 2-mL tube containing 95% methanol. The samples were incubated in the dark at 4°C for 72 h, and five replicates were set up for each sample. After complete extraction of flavonoids, 0.1 mL of the supernatant was withdrawn, followed by sequential addition of 0.2 mL of 5% $NaNO_2$, 0.3 mL of 10% $AlCl_3$, and 1.0 mL of 1 mol L^{-1} NaOH. The mixture was then diluted to a final volume of 3.8 mL with ultrapure water, thoroughly mixed, and allowed to stand for 5 min. Absorbance was measured at 510 nm using a *UV-2450* spectrophotometer (*Shimadzu*, Tokyo, Japan), with 95% methanol as the blank. Flavonoid content was quantified based on a standard curve established using serial dilutions of catechins.

Phenolic content: Phenolic content was determined by the method of Ainsworth and Gillespie (2007) with appropriate modifications. Phenolics in plant leaves were extracted using the same procedure as for flavonoids. After complete extraction of phenolics, 0.25 mL of the extract was transferred to a new tube, followed by the addition of 0.5 mL of 10% Folin solution. Then, 1.0 mL of a 0.7 mmol L^{-1} Na_2CO_3 solution was added, and the mixture was thoroughly mixed to ensure color development. After the solution was mixed and left to stand, the absorbance value was measured at 765 nm using a *UV-2450* spectrophotometer (*Shimadzu*, Tokyo, Japan), and 95% methanol was used as the blank. Total phenolic content was quantified based on a standard curve generated using serial dilutions of gallic acid.

Total antioxidant capacity (TAC): The determination of TAC in leaves was based on the method of Saha *et al.* (2008) with appropriate modifications. Leaf extraction for TAC was carried out using the same procedure as that used for flavonoids. The assay is based on the scavenging of the DPPH radical (1,1-diphenyl-2-trinitrophenylhydrazine, 1,1-diphenyl-2-picrylhydrazyl). Briefly, 0.1 mL of the extract was mixed thoroughly with 3.0 mL of a 100 μmol L^{-1} DPPH solution in 95% methanol. The mixture was incubated in the dark at room temperature for 5 min. Absorbance was measured at 517 nm using a *UV-2450* spectrophotometer (*Shimadzu*, Tokyo, Japan), with 95% methanol serving as the blank. A standard curve was established by gradient dilution of DPPH solution, and the ability of the samples to scavenge DPPH was calculated.

Gas-exchange parameters: To ensure optimal photosynthetic status, gas-exchange parameters were measured on consecutive clear mornings (8:30–11:30 h) using a portable infrared gas analyzer, *Li-6400* (*Li-COR*, *Inc*., Lincoln, NE, USA), in three different habitats. Before measurement, the instrument was calibrated and verified for proper operation. During measurement, the ambient air temperature averaged 22°C, the relative humidity was 48%, and the atmospheric CO_2 concentration was 400 µmol mol^{-1}. The CO_2 concentration in the leaf chamber was maintained at ambient levels. Leaf chambers were equipped with LED light sources (red:blue = 9:1). Each leaf was pre-illuminated with a saturated light intensity of 800 µmol(photon) m^{-2} s^{-1} for 5–8 min. Net photosynthetic rate (P_N) was recorded once instrument readings stabilized.

Chlorophyll fluorescence parameters: Leaf chlorophyll fluorescence was determined using a *PAM-2500* portable modulated chlorophyll fluorometer (*Waltz*, Germany). Measurements were conducted under clear-day conditions on healthy *S. trilobata* leaves collected from three different habitats. Before measurement, leaves were dark-adapted for 30 min. The initial fluorescence (F_o) was then measured by applying a measuring light of less than 0.05 µmol(photon) m^{-2} s^{-1}. A saturation pulse of 9,000 µmol(photon) m^{-2} s^{-1} was applied for 0.8 s to obtain the maximum fluorescence (F_m) and variable fluorescence (F_v). The maximal quantum yield of PSII photochemistry (F_v/F_m) for dark-adapted leaves was automatically calculated by the instrument. Subsequently, the instrument's actinic light was set to 800 µmol(photon) $m^{-2} s^{-1}$ to determine the steady-state chlorophyll fluorescence parameters. After the measurements were completed, the actinic light was turned off. Main fluorescence parameters were obtained from the instrument's report file, including F_v/F_m, the actual photochemical quantum yield of PSII ($Y_{(II)}$), the electron transfer rate (ETR), the quantum yield of regulatory energy dissipation at PSII ($Y_{(NPQ)}$), and the quantum yield of unregulated energy dissipation at PSII ($Y_{(NO)}$).

Data analyses: All experimental data were preliminarily processed in *Microsoft Excel 2016* and subsequently analyzed using *SPSS 18.0*. One-way analysis of variance (*ANOVA*) was performed to assess differences between groups, and *Duncan*'s multiple comparisons were used to test the significance of differences in physiological indices of *S. trilobata* leaves in different habitats, with the test significance level of 0.05. Plotting of the data was done using *Sigmaplot 14*. All data are expressed as mean ± standard error (SE). Bars sharing different lowercase letters within each figure indicate statistically significant differences ($P<0.05$). Principal component analysis (PCA) was conducted using *Canoco* software to explore multivariate relationships among *S. trilobata* leaf traits across habitats. Factor loadings of S. *trilobata* on the first two principal component (PC) axes were compared to evaluate group separation. Structural equation modelling (SEM) was performed using *AMOS 22.0* (*IBM SPSS AMOS*, *IBM Corporation*, Armonk, NY, USA) (Grace *et al.* 2010). The initial SEM was constructed based on the presumed importance of functional traits, photoprotective and photosynthetic capacities of *S. trilobata* divaricate leaves for the growth of *S. trilobata*. To evaluate the relative importance of these physiological indices of *S. trilobata* in regulating growth in different habitats, by default, principal component analysis was carried out on the photosynthesis and photoprotective substance indices of *S. trilobata* in different habitats and extraction the principal component 1 (PC1), thus quantifying the correlation among *S. trilobata*, growth, leaf functional traits, photoprotective capacity, and photosynthetic capacity in different habitats. Standardized total effect of explanatory variables on different habitat were assessed by SEM. We then tested alternative SEM models using stepwise removal of nonsignificant pathways. The best-fitting model was determined using the maximum likelihood χ^2 test, the root mean square error of approximation (RMSEA) index, and the goodness-of-fit index (CFI) (Grace *et al.* 2010). The model was considered to pass the test, and the model results were considered credible when the model χ^2 test satisfied $P>0.05$ and RMSEA ≤ 0.05.

Results

Functional traits and growth: The growth of individual *S. trilobata* plants during the experimental period varied significantly among habitats, as reflected in plant biomass, height, and morphological traits of the second and third stem nodes (including length and diameter). *S. trilobata* growing in farmland had significantly greater aboveground biomass and longer second and third internodes, followed by the riverside, and the smallest in the woodland (Fig. 1*A–C*). In contrast, plant height and stem node diameters were the greatest in the riverside habitat, intermediate in farmland, and smallest in the woodland (Fig. 1*D*,*E*,*M*). FW and FW/BW were significantly higher in farmland-grown plants; no significant difference was observed between woodland and riverside plants (Fig. 1*F*,*H*). BW was the highest in the riverside habitat and the lowest in farmland (Fig. 1*G*). LMA and LT followed identical trends across habitats: the highest in farmland, intermediate at the riverside, and the lowest in woodland (Fig. 1*J*,*L*). SLA showed the inverse pattern to LMA (Fig. 1*I*). LDMC did not differ significantly between habitats (Fig. 1*K*).

Photosynthetic pigment content: The photosynthetic pigment contents of *S. trilobata* leaves differed significantly between the three habitats. Chlorophyll *a* (Chl *a*) content was the highest in woodland, intermediate in farmland, and the lowest at the riverside (Fig. 2*A*). The content of Chl *b* and total chlorophyll [Chl (*a*+*b*)] followed the same pattern, with significantly higher concentrations in woodland than in farmland or riverside; however, no significant difference was observed between farmland and riverside (Fig. 2*B*,*D*). In contrast, the Chl *a*/*b* ratio was the lowest in woodland, showing an inverse trend to Chl *b* and Chl (*a*+*b*) (Fig. 2*C*). Carotenoids (Car) content did not differ significantly between woodland

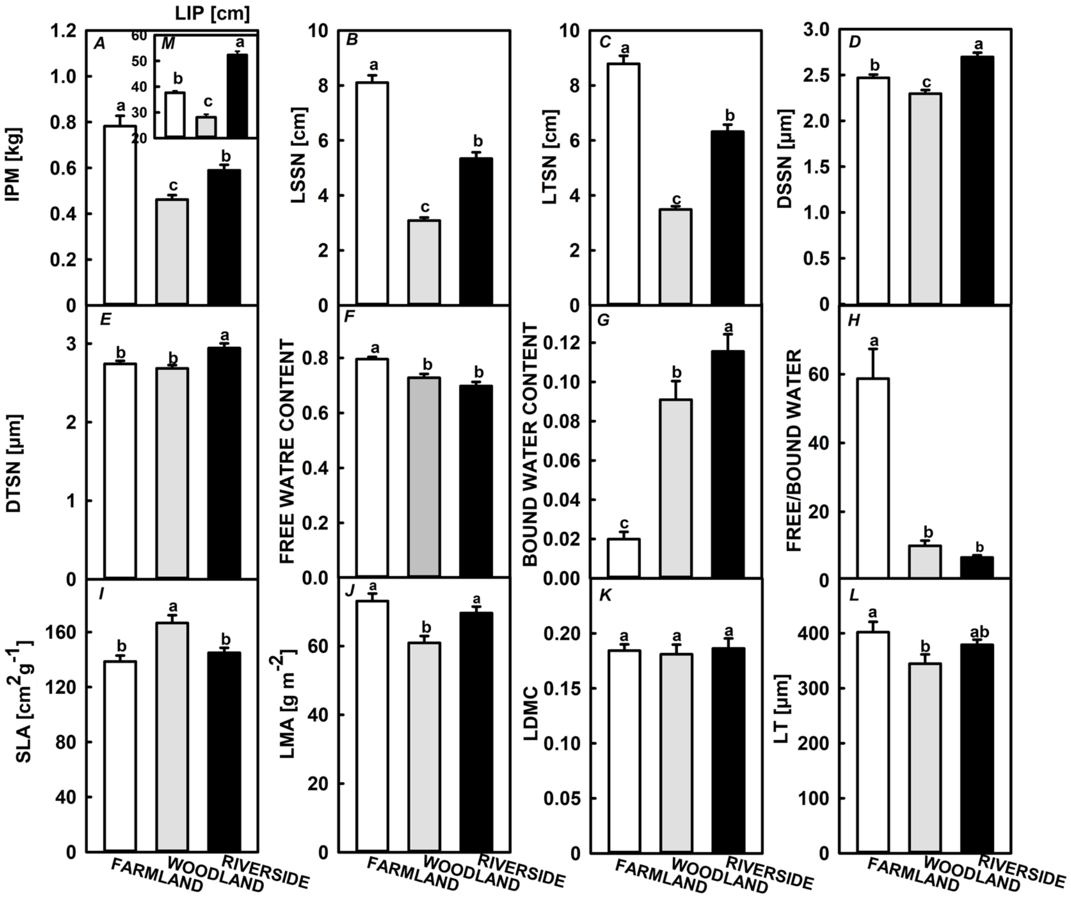

Fig. 1. Growth of *Sphagneticola trilobata* (n = 28–72) in three habitats (farmland, woodland, and riverside), including: individual plant mass (IPM) (*A*), length of second stem node (LSSN) (*B*), length of third stem node (LTSN) (*C*), diameter of second stem node (DSSN) (*D*), and diameter of third stem node (DTSN) (*E*). Functional traits of *S. trilobata* leaves (n = 15) in three habitats including: free water content (*F*), bound water content (*G*), free/bound water (*H*), specific leaf area (SLA) (*I*), leaf mass per area (LMA) (*J*), dry matter content (LDMC) (*K*), leaf thickness (LT) (*L*) and length of individual plant (*M*). All data are presented as mean ± standard error (SE). *Different letters* above bars indicate statistical significance (P<0.05).

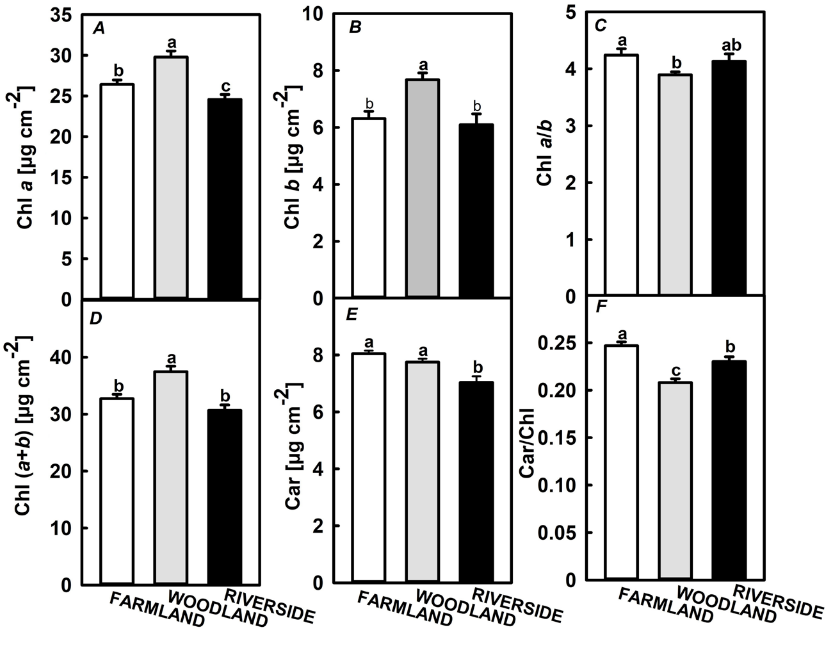

Fig. 2. Comparison of photosynthetic pigment content of *Sphagneticola trilobata* leaves in three habitats (farmland, woodland, and riverside). Includes: chlorophyll *a* (Chl *a*) (*A*), chlorophyll *b* (Chl *b*) (*B*), chlorophyll *a*/*b* (Chl *a*/*b*) (*C*), total chlorophyll content [Chl (*a*+*b*)] (*D*), carotenoids (Car) (*E*), and carotenoids/total chlorophyll (Car/Chl) (*F*). All data are presented as mean ± standard error (SE). *Different letters* above bars indicate statistical significance (P<0.05).

and farmland but was significantly lower at the riverside (Fig. 2*E*). The Car/Chl ratio was the highest in farmland, intermediate at the riverside, and the lowest in woodland (Fig. 2*F*).

Photoprotective substance content and photosynthetic capacity: The contents of antioxidant substances in *S. trilobata* leaves differed significantly between habitats. Flavonoid content, phenolic content, and total antioxidant capacity were the highest in farmland, intermediate at the riverside, and the lowest in woodland (Fig. 3). In addition, the heat dissipation capacity in the leaves of *S. trilobata* grown in different habitats also varied, but the trend was different from that of antioxidant content, showing the highest $Y_{(NPQ)}$ and $Y_{(NO)}$ growing by the riverside, followed by those growing in the woodland, and the lowest in farmland (Fig. 4*B*,*C*). The maximal quantum yield of PSII photochemistry (F_v/F_m) showed no significant difference between riverside and woodland plants, but both were significantly higher than in farmland plants. In contrast, ETR and $Y_{(II)}$ were the highest in farmland and the lowest at the riverside (Fig. 4*D*,*E*). P_N mirrored ETR and $Y_{(II)}$, being the highest in farmland and lowest at the riverside (Fig. 4*F*).

Principal component analysis of physiological indicators: Principal component analyses (PCA) were conducted on leaf functional traits, photosynthetic parameters, and photoprotective physiological parameters of *S. trilobata* in three habitats. Two principal components were extracted from the leaf functional traits. The first principal component (PC1) explained 76.4% of the total variation and was primarily loaded by SLA, LSSN, LTSN, and LMA. The second principal component (PC2) explained 13.6% of the variation and was primarily loaded by LIP, DSSN, DTSN, BW, and FW. PC1 was interpreted as reflecting growth-related variation, whereas PC2 reflected metabolic capacity (Fig. 5*A*). For photosynthetic parameters, two principal components were also extracted. PC1 accounted for 94.5% of the total variance and was strongly associated with ETR, $Y_{(II)}$, Car, P_N, and FW/BW. Thus, PC1 represented integrated photosynthetic capacity (Fig. 5*B*). For photoprotective parameters, two principal components were extracted. PC1 explained

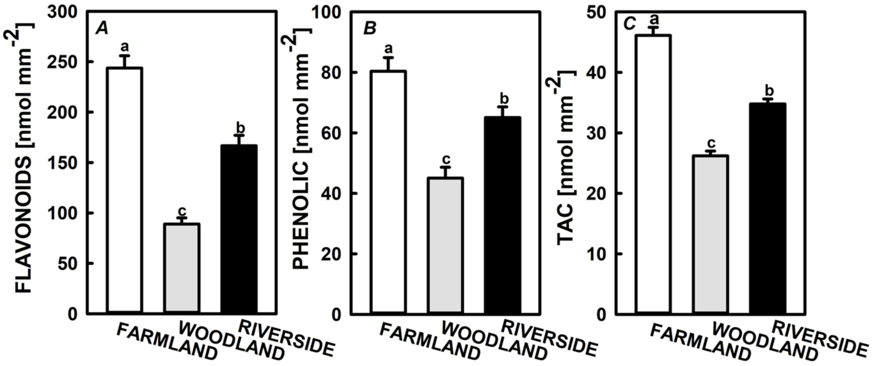

Fig. 3. Changes in antioxidant substance content of *Sphagneticola trilobata* leaves in three habitats (farmland, woodland, and riverside). Including: flavonoid content (*A*), phenolic content (*B*), and total antioxidant capacity (TAC) (*C*). All data are presented as mean ± standard error (SE). *Different letters* above bars indicate statistical significance ($P<0.05$).

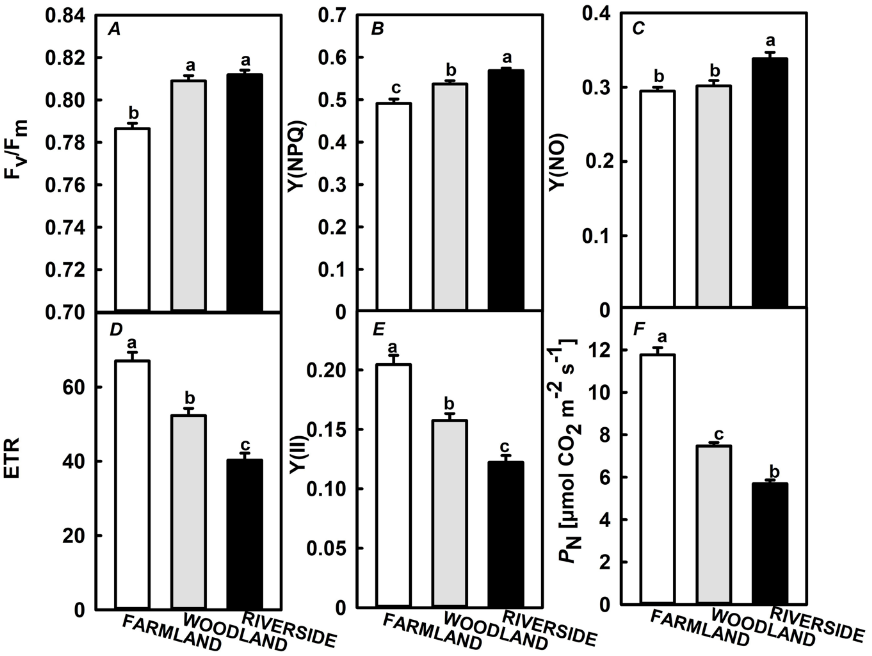

Fig. 4. Changes in chlorophyll fluorescence parameters (*n* = 30–32) and photosynthetic rate (*n* = 15) of *Sphagneticola trilobata* leaves in three habitats (farmland, woodland, and riverside). Including: the maximum potential photochemical efficiency (F_v/F_m) (*A*), quantum yield of regulatory energy dissipation at PSII ($Y_{(NPQ)}$) (*B*), quantum yield of unregulated energy dissipation at PSII ($Y_{(NO)}$) (*C*), electron transfer rate (ETR) (*D*), actual photochemical efficiency of PSII ($Y_{(II)}$) (*E*), and maximum net photosynthetic rate (P_N) (*F*). All data are presented as mean ± standard error (SE). *Different letters* above bars indicate statistical significance ($P<0.05$).

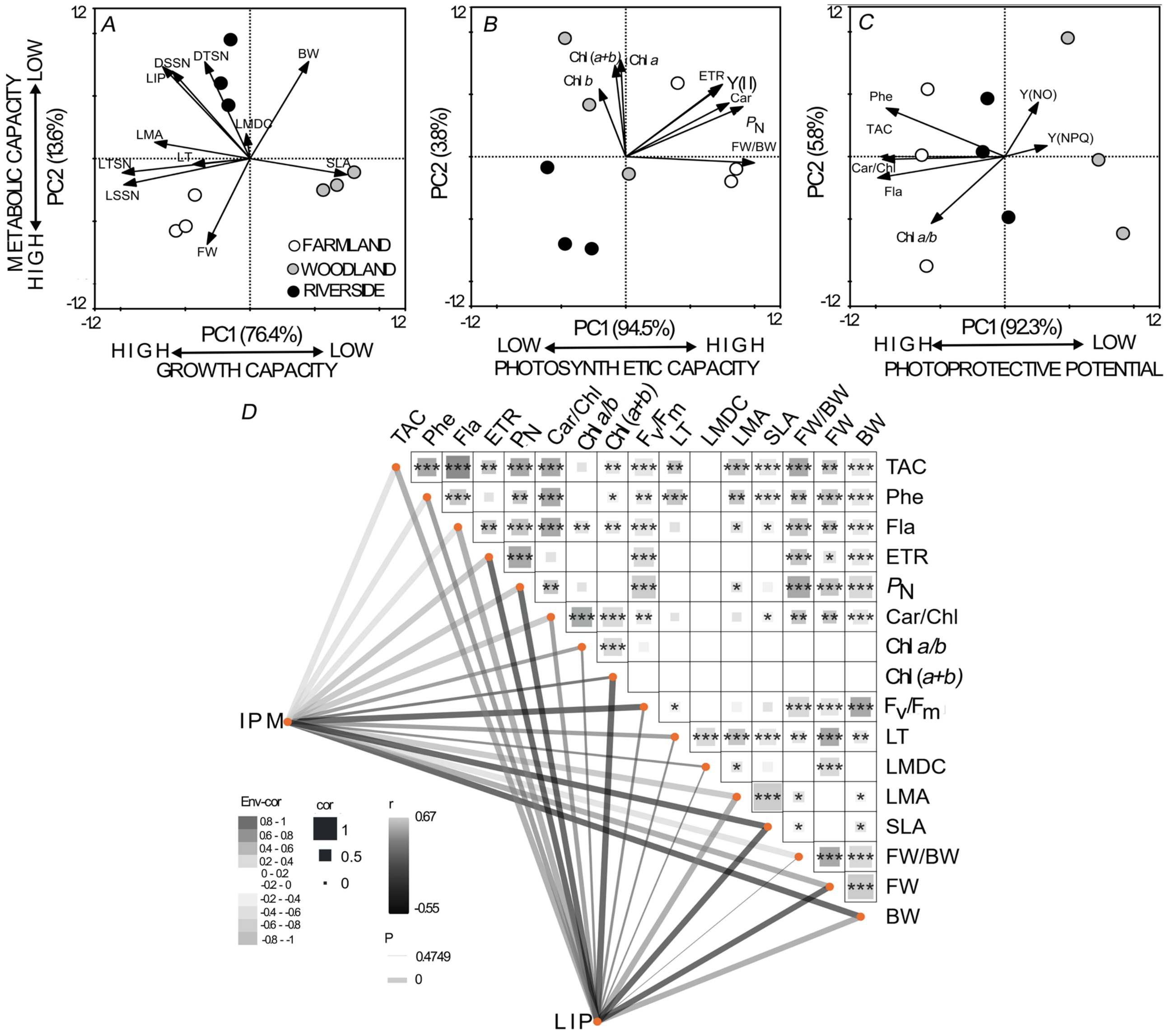

Fig. 5. Principal component analysis of five growth indicators and six leaf functional traits (*A*), principal component analysis of eight physiological indicators related to photosynthesis (*B*), and principal component analysis of seven physiological indicators related to photoprotective capacity (*C*) of *Sphagneticola trilobata* in three habitats (farmland, woodland, and riverside). (*D*) Heatmap showing the correlation network of *S. trilobata* growth increment with leaf physiological indicators. Six growth indicators include: IPM, LIP, LSSN, LTSN, DSSN, DTSN; six leaf functional traits include: FW, BW, SLA, LMA, LDMC, and LT; and eight photosynthesis physiological indices include: FW/BW, Chl *a*, Chl *b*, Chl (*a*+*b*), Car, ETR, $Y_{(II)}$, and P_N; seven physiological indices related to photoprotective capacity include: flavonoid content (Fla), phenolic content (Phe), TAC, Chl *a*/*b*, Car/Chl, $Y_{(NPQ)}$, $Y_{(NO)}$.

92.3% of the trait variation and was predominantly loaded by Car/Chl, Phe, Fla, TAC, and $Y_{(NPQ)}$. Hence, PC1 represented photoprotective potential (Fig. 5*C*). The correlation network heatmap further supported these PCA interpretation (Fig. 5*D*).

Structural equation modeling of physiological indicators: To comprehensively explore the drivers of growth variation in *S. trilobata* in different habitats, we applied structural equation modelling (SEM) to examine relationships among latent variables representing leaf functional traits PC1, photosynthetic capacity PC1, antioxidant substance content PC1, heat dissipation PC1, F_v/F_m, and growth PC1. Analyses were conducted for three pairwise habitat transitions: from farmland to woodland, from woodland to riverside, and from farmland to riverside (Fig. 6). It was found that the growth environment changes from farmland to understory had significant negative effects on leaf functional traits PC1 (–0.60), photosynthetic capacity PC1 (–0.97), antioxidant substance content PC1 (–0.96), and growth PC1 (–0.96), but had significant positive effects on heat dissipation PC1 (0.75) (Fig. 6*A*). The change of growth environment from woodland to riverside had a significant negative effect on photosynthetic capacity PC1 (–0.81). Although negative effects were also observed for leaf functional traits PC1 and heat dissipation

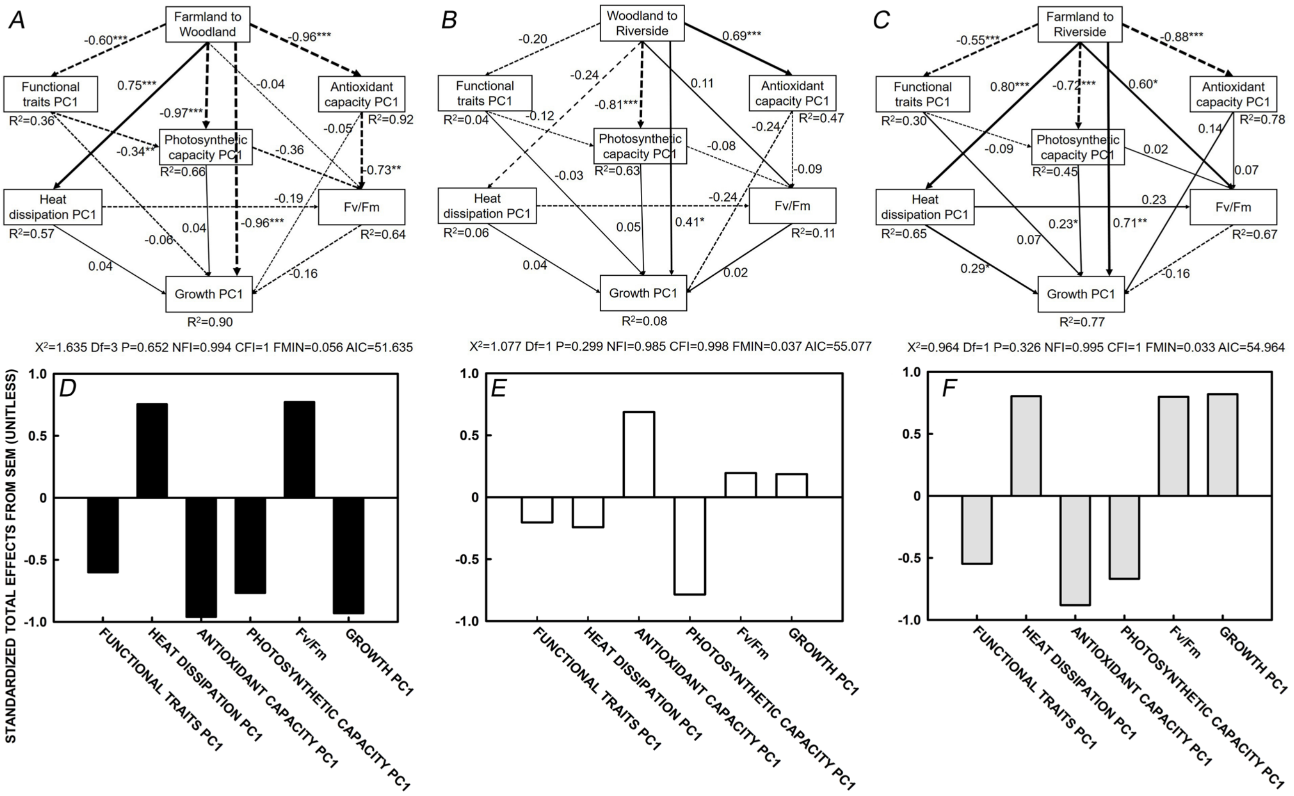

Fig. 6. Structural equation modelling (SEM) of the relationship between functional traits PC1, photosynthetic capacity PC1, heat dissipation PC1; antioxidant capacity PC1, F_v/F_m and growth PC1 of *Sphagneticola trilobata* leaves under different habitat variations [farmland to woodland (*A*, *D*), woodland to riverside (*B*, *E*), farmland to riverside (*C*, *F*)]. The different factors showed direct and indirect effects (*A–C*) and standardized total effects (*D–E*) on the growth of *S. trilobata*. Standardized path coefficients for effect sizes of potential causal variables are indicated by the numbers adjacent to the arrows. *Solid arrows* indicate positive effects and *dashed arrows* indicate negative effects. The thicker the arrows, the more significant. The numbers adjacent to boxes of response variables denote the explained variance (R^2). Functional traits PC1: principal component 1 extracted from FW, LMDC, LMA, LT and FW/BW; photosynthetic capacity PC1: principal component 1 extracted from Chl *a*, Chl *b*, Chl (*a*+*b*), Car, Chl *a*/*b*, P_N, ETR, and $Y_{(II)}$; heat dissipation PC1: principal component 1 extracted from Car/Chl, $Y_{(NPQ)}$, and $Y_{(NO)}$; antioxidant capacity PC1: principal component 1 extracted from flavonoids, phenolic, and total antioxidant capacity; growth PC1: principal component 1 extracted from length of individual plant, length of second stem node, length of third stem node, diameter of second stem node and diameter of third stem node. *Colors* indicate different habitat variations. * indicates significant difference at the 0.05 level. ** indicates significant difference at the 0.01 level. *** indicates significant difference at the 0.001 level.

PC1, these were nonsignificant. In contrast, antioxidant substance content PC1 (0.69) and growth PC1 (0.41) had significant positive effects (Fig. 6*B*). In addition, the trend of environmental changes in the growth of *S. trilobata* from farmland to riverside was consistent with that from farmland to woodland, with significant negative effects on leaf functional traits PC1 (–0.55), photosynthetic capacity PC1 (–0.72), and antioxidant substance content PC1 (–0.88), and significant positive effects on heat dissipation PC1 (0.80) and F_v/F_m (0.60), and growth PC1 exerted positive effects (0.71) (Fig. 6*C*). When combining the direct and indirect effects of individual factors, four of the six factors retained in the SEM (leaf functional traits PC1, antioxidant content PC1, photosynthetic capacity PC1, and growth PC1) had a negative effect and two (heat dissipation PC1 and F_v/F_m) positive effect on farmland to woodland environmental change (Fig. 6*D*); and three had a negative effect on woodland to riverside environmental change (leaf functional traits PC1, photosynthetic capacity PC1 and heat dissipation PC1) and three positive effects (antioxidant content PC1, F_v/F_m, and growth PC1) (Fig. 6*E*); and three negative effects (leaf functional traits PC1, antioxidant content PC1, and photosynthetic capacity PC1) and three positive effects (heat dissipation PC1, F_v/F_m, and growth PC1) (Fig. 6*F*).

Discussion

Effects of different habitat environments on the growth of the invasive plant *S. trilobata*: Invasive plants can successfully colonize diverse environments because they can adjust their physiological and morphological traits to enhance adaptation and stress tolerance (Blonder *et al.* 2018, Carboni *et al.* 2018, Boonman *et al.* 2020). However, even successful invaders exhibit varying functional and physiological responses under different environmental conditions, which may drive variation in invasion potential across habitats. Such adaptive plasticity has been documented in many invasive species, including *S. trilobata*, which shows distinct response patterns in different resource environments, further strengthening its invasive capacity (Cai *et al.* 2021a,b; 2024; Zhang *et al.* 2021, 2024a,b; Kato-Noguchi and Kato 2025). Our study revealed clear growth differences between *S. trilobata* individuals grown in the three habitats. Plants from farmland exhibited the highest biomass and thus the strongest growth performance, followed by those from riverside habitats, whereas woodland plants showed the poorest growth (Fig. 1*A*). Specifically, farmland-grown individuals had the greatest individual mass and the longest second and third internodes (Fig. 1*A–C*). Principal component analysis (Fig. 5*A*) and structural equation modeling (Fig. 6) further confirmed that invasive plants had greater invasive potential in farmland than in riverside and woodland habitats. In contrast, plant height and stem internode diameter (second and third nodes) were significantly greater in riverside than in farmland habitats (Fig. 1*D*,*E*,*M*). This pattern may be explained by a shift in growth strategy: upon reaching a threshold height, *S. trilobata* likely reallocates more resources to clonal lateral spread and ramet production rather than vertical growth. Clonal propagation is a well-established trait that enhances competitive advantage in heterogeneous environments (Yu *et al.* 2009, You *et al.* 2014), improves ramet establishment under stress (Roiloa *et al.* 2014), and boosts performance of invasive alien plant species (Xu *et al.* 2010, Wang *et al.* 2016). Conversely, riverside plants prioritize vertical development, resulting in taller stature and thicker stems. This morphological divergence also explains the positive total effect of the transition from farmland to riverside on growth PC1 in the structural equation model (Fig. 6*C*,*F*). In woodland habitats, low-light conditions constrain photosynthetic capacity and limit growth, thereby reducing *S. trilobata*'s invasion potential. Thus, not all habitats confer equal growth advantages. Invasion success is strongly context-dependent and varies substantially with local environmental conditions.

Differences in leaf functional traits: In addition, the reason for the strong invasion potential of the invasive plant *S. trilobata* in farmland habitats is related to the strong plasticity of its functional traits. Abiotic environmental factors are known to shape the diversity and variability of plant functional traits at spatial scales (Bruelheide *et al.* 2018, Wieczynski *et al.* 2019). Our findings support this view, revealing significant differences in the leaf functional traits of *S. trilobata* across different habitats. Specifically, plants grown in farmland exhibited the highest values for leaf FW, free/bound water ratio, LMA, and LT, followed by those in riverside habitats, with woodland plants showing the lowest values (Fig. 1*F*,*H*,*J*,*L*). A study of a large global dataset of leaf characteristics confirms that invasive plants tend to have a higher competitive advantage by regulating a combination of leaf functional traits, such as SLA, leaf life span, and LT (Wright *et al.* 2004, Leishman *et al.* 2007). The relationship between invasive plants and their invasiveness is known to be context-dependent, varying with the invaded environment (Lambrecht 2002, Funk and Vitousek 2007). This explains the superior growth performance of *S. trilobata* in farmland (Fig. 1*A*). Farmland presents both opportunities and challenges: while it provides ample resources such as water, nutrients, and light, it also subjects plants to periodic high-temperature and high-light stress. In response, *S. trilobata* modulates traits such as free/bound water content, LMA, and LT to sustain high metabolic activity and growth rates under these conditions. This adaptive mechanism is further corroborated by principal components analysis of leaf functional traits and growth capacity (Fig. 5*A*), as well as by structural equation modelling, which quantifies the direct, indirect, and total standardized effects of multiple physiological drivers on *S. trilobata* growth (Fig. 6).

Relationship between photoprotective capacity and growth of leaves: The observed shifts in leaf functional traits alone are insufficient to explain the rapid growth of *S. trilobata* in farmland, and the high synthesis of some photoprotective compounds in leaves is a key mechanism sustaining this growth advantage. The growth of plants in different habitats is not only influenced by their genetic material, but also by changes in habitat environmental factors (Kunstler *et al.* 2016, Boonman *et al.* 2020). It has been shown that high-temperature stress can inhibit chlorophyll synthesis and reduce photosynthetic rates, leading to reactive oxygen species accumulation and ultimately impairing plant development and height (Cai *et al.* 2020). Similarly, stresses such as moisture, drought, low light, and high light can cause stress throughout plant growth (Hussain *et al.* 2018, Sun *et al.* 2015, Zhang *et al.* 2021). To cope with such environmental pressures, invasive plants like *S. trilobata* employ various photoprotective strategies. These include increasing the activity of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), and ascorbate peroxidase (APX) (Cai *et al.* 2021b), decrease in the maximum conversion efficiency of PSII primary light energy, increase in intracellular proline content and soluble sugars content (Zhang *et al.* 2021), synthesis of antioxidant substances (Cai *et al.* 2021b, Zhang *et al.* 2021), accumulation of anthocyanin glycosides (Cai *et al.* 2021a), and increased heat dissipation (Cai *et al.* 2021b, Zhang *et al.* 2021). These coordinated adjustments indicate that *S. trilobata* tailors its photoprotective strategy to habitat-specific stress regimes. Consistent with this, flavonoid content, phenolic content, total antioxidant capacity (Fig. 3), and Car/Chl (Fig. 2*F*) were the highest in farmland-grown *S. trilobata*, intermediate in riverside plants, and the lowest in woodland plants. This implies that *S. trilobata* growing in farmland would synthesize more antioxidants and heat dissipation capacity contributed by Car/Chl to exercise photoprotection. In contrast, riverside plants mainly relied on the dissipation mechanism involved in dissipating excess light energy from photosynthetic organs to achieve photoprotection, so it shows higher $Y_{(NO)}$ and $Y_{(NPQ)}$ (Fig. 4*B*,*C*). Nevertheless, they also maintained relatively high antioxidant contents (Fig. 3). However, the results of F_v/F_m showed (Fig. 4*A*) that the leaves of *S. trilobata* growing in farmland were significantly lower than those of the riverside and the woodland, and the F_v/F_m ratio can be used as an indicator to judge the photoinhibition (Zhang *et al.* 2016, Poudyal *et al.* 2018). This is further evidence that the farmland growing environment is both an opportunity and a challenge for the growth of the invasive plant *S. trilobata*. Principal component analysis showed that *S. trilobata* growing in farmland had higher photoprotection potential and greater growth capacity. The changes of antioxidant substances contents in different habitats were consistent with the trend of growth increment (Fig. 5*A*,*C*). In addition, structural equation modeling revealed significant environmental effects on the antioxidant capacity (PC1) of *S. trilobata*. Specifically, the shift from farmland to woodland showed a strong negative effect (–0.96), while the shift from woodland to riverside showed a positive effect (0.69). The change from farmland to riverside also exhibited a significant negative effect (–0.88) (Fig. 6*A–C*). These results indicate that the photoprotective capacity provided by antioxidant substances guarantees a stronger tolerance of high temperature and high light in agricultural fields, thus conferring a stronger competitive advantage to *S. trilobata* in farmland habitats. However, it should be noted that the photoprotective substances analyzed in this study were not comprehensive. Changes in other photoprotection-related indicators, such as antioxidant enzyme activity and soluble sugar content, remain unknown. Thus, future work must integrate broader physiological metrics to systematically link photoprotective capacity with invasion potential.

Relationship between photosynthetic capacity and leaf growth: In addition, photosynthesis underpins plant growth and development and is the primary source of biomass accumulation (Zhang *et al.* 2017, Jiang *et al.* 2020). The growth differences observed in *S. trilobata* in different habitats are closely linked to variation in its photosynthetic capacity. Our results showed that, among the three habitats, *S. trilobata* from farmland with higher photosynthetic capacity showed the highest ETR, $Y_{(II)}$, and P_N (Fig. 4*D–F*), followed by woodland plants and then riverside plants. The ecological environment shapes the distribution of suitable habitats for plant species at different spatial scales (Wisz *et al.* 2013, Carboni *et al.* 2018). This environmental influence is also reflected in photosynthetic pigment trends. Specifically, *S. trilobata* in woodland showed the highest Chl *a*, Chl *b*, Chl (*a*+*b*), and the lowest Chl *a*/*b* and Car/Chl. In contrast, Chl *b*, Chl (*a*+*b*), and Chl *a*/*b* did not differ significantly between farmland and riverside plants (Fig. 2). This is closely related to their growing habitats because the woodland is a low-light environment, so *S. trilobata* needs to increase its light-trapping pigment and leaf area to improve its light-trapping capacity, which is why *S. trilobata* has the largest specific leaf area in the woodland (Fig. 1*I*). Principal component analysis confirmed that farmland-grown *S. trilobata* had higher photosynthetic capacity and greater growth capacity (Fig. 5*A*,*B*). The correlation network heatmap further supports the principal component analysis (Fig. 5*D*). Structural equation modeling revealed that the growth environment changes from farmland to woodland, woodland to riverside, and farmland to riverside had significant negative effects on the photosynthetic capacity PC1 of *S. trilobata* (–0.97, –0.81, and –0.72, respectively) (Fig. 6*A–C*). Collectively, these findings indicate that higher photosynthetic capacity sustains a greater growth potential in *S. trilobata*, thereby enhancing its adaptability in farmland habitats. Notably, the relationship between photosynthetic rate and plant acclimation remains important in trait correlation studies (Liu and El-Kassaby 2019). Differences in light, temperature, and soil nutrients likely drive the physiological divergence between riverside and farmland plants. Compared to riverside, farmland provides higher soil nutrient availability, imposes greater thermal stress, and subjects plants to lower light limitation. Due to the specific heat capacity of water, riverside microclimates buffer air temperature fluctuations. But this also elevates local light intensity due to reduced atmospheric scattering. Nevertheless, riverside plants exhibit lower leaf trait plasticity, photoprotective capacity, and photosynthetic performance than farmland plants, resulting in a significantly slower growth. Furthermore, *S. trilobata* is a thermophilic species well adapted to high-temperature, high-light environments, requiring substantial acclimation when exposed to cooler, low-light conditions (Sun *et al.* 2015, Cai *et al.* 2021b), which explains why *S. trilobata* had the lowest growth in woodland.

Conclusions: In this study, *S. trilobata* exhibited variations in leaf functional traits, photosynthetic capacity, and photoprotective strategies across different habitats, reflecting its adaptability and tolerance to diverse environmental stresses. Greater plasticity in functional traits (including FW, BW, SLA, LMA, LDMC, and LT) and higher photosynthetic capacity (including P_N, ETR, $Y_{(II)}$, and photosynthetic pigment) indicate enhanced adaptive ability in this invasive species. Additionally, a more flexible and robust photoprotective capacity (including flavonoid content, phenolic content, TAC, Car/Chl, $Y_{(NPQ)}$, and $Y_{(NO)}$) confers greater stress tolerance. These integrated physiological and photoprotective advantages explain why *S. trilobata* from farmland achieved the highest biomass, including individual plant mass and second/third stem internode length. Plants from the riverside habitat maintained relatively high growth, driven primarily by superior heat dissipation and photoprotective capacity contributed by elevated photoprotective compound accumulation. In contrast, the low-light woodland environment, despite supporting moderately high photosynthetic capacity, failed to compensate for the limited photoprotective capacity, resulting in minimal growth. Critically, farmland-grown plants simultaneously maintain high photosynthetic capacity and high contents of photoprotective compounds, suggesting a synergistic enhancement strategy. We speculate that under chronic stress, plants face a resource allocation trade-off between photosynthetic investment and photoprotection. Future experiments along controlled resource gradients will help clarify the dynamic balance between these processes under varying stress intensities. Based on our findings, *S. trilobata* exhibits the strongest invasion potential in farmland, intermediate potential at the riverside, and the weakest in woodland. This study provides empirical evidence for predicting the spatial distribution and habitat-specific invasion risk of the alien invasive plant *S. trilobata*. However, plant age and initial physiological condition were not standardized across the three habitats, which represents a potential confounding factor. In future work, we will consider using plants sown at the same time or clones of the same age to isolate the effect of the habitat better.

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