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Revealing differences in the invasiveness of *Sphagneticola trilobata* under different light environments based on physiological and morphological plasticity

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Abstract

Studies of the physiological and morphological characteristics of invasive plants contribute to understanding their invasive capacity. However, it remains unclear whether the same invasive plant species relies equally on morphological and physiological traits to enhance its invasiveness potential across different light habitats. In this study, the invasive plant *Sphagneticola trilobata* (L.) Pruski was used to examine eight morphological traits and nine physiological traits of the leaf under contrasting light conditions. Results revealed that under full light, growth, biomass, and all physiological traits, as well as most morphological traits of *S. trilobata* were significantly higher than those under low-light conditions. This suggests that *S. trilobata* achieves invasion success by altering its morphological and physiological traits. Notably, under full light, the species exhibited higher physiological plasticity but lower morphological plasticity. The study confirms that *S. trilobata* possesses greater invasive potential under full light, further underscoring the importance of physiological plasticity during the invasion process.

Keywords: full light and low light; invasion potential; invasive plants; morphological traits; physiological traits.

Introduction

Compared to native species, invasive species often exhibit greater environmental adaptability, which enhances their competitiveness for habitat resources (Carroll 2007, Jardeleza *et al*. 2022, Sharma *et al*. 2024). Morphological and physiological plasticity are key strategies contributing to plant invasion success, and high plasticity is widely regarded as an important predictor of invasive potential (Hou *et al*. 2015, Musso *et al*. 2021). This is because plasticity in morphological and physiological traits enables invasive plants to acquire limited resources more effectively and colonize a wide range of novel environments (Funk 2008, Moroney *et al*. 2013, Pepe *et al*. 2022). Previous studies suggest that the strong invasiveness of these plants may arise from their capacity to adjust physiological or morphological traits in response to spatial variable light availability or temporal fluctuations in water and nutrient conditions (Davis *et al*. 2000, Song *et al*. 2007, Allred *et al*. 2010, Liu *et al*. 2025). However, the morphological and physiological plasticity may contribute to invasion through distinct mechanisms (Grime and Mackey 2002, Hou *et al*. 2015). Most current studies focus solely on comparing morphological and physiological

Highlights

- Invasive plants facilitate invasion through morphological and physiological plasticity
- Physiological plasticity plays a more critical role in the invasion process
- The cost of physiological plasticity is lower than that of morphological plasticity

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Abbreviations: BW – bound water content; Car/Chl – carotenoids to total chlorophyll ratio; Chl – total chlorophyll; ETR – electron transfer rate; Flav – flavonoids; F_v/F_m – maximum quantum yield of PSII photochemistry; FW – free water content; LDMC – leaf dry matter content; LMA – leaf mass per area; LT – leaf thickness; Phen – 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.

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plasticity between native and invasive species, although the link between plasticity and invasiveness has been well established (Wang *et al*. 2017a, Zhang *et al*. 2022, Liu *et al*. 2024, Sharma *et al*. 2024). Little research has addressed how plasticity varies across different environments within the same invasive species. This gap hinders accurate assessment of the invasive potential of invasive plants in different habitats from the perspective of morphological and physiological plasticity.

Morphological and physiological plasticity provide valuable insights into the ecological strategies, invasiveness, and environmental impacts of invasive plants (Drenovsky *et al*. 2012, Liu *et al*. 2024). The capacity of invasive plants to exploit resources across habitats is shaped by variation in their functional traits, which is often closely associated with invasive potential (Gallagher *et al*. 2015, Sharma *et al*. 2024). Therefore, quantifying variation in these traits and their plasticity is critical for understanding invasion processes and assessing invasion potential (Fox *et al*. 2019). Changes in leaf morphological traits, such as leaf shape, leaf area, biomass, water content, and specific leaf area (SLA), can significantly affect growth and development, especially in response to fluctuations in environmental resources (Akram *et al*. 2022, Sharma *et al*. 2024). Leaf thickness affects plant growth, carbon balance, and water-use efficiency, and serves as a key determinant of a plant's ability to establish and persist in novel environments (Damián *et al*. 2020). Similarly, invasive plants may gain a competitive advantage through physiological characteristics associated with high photosynthetic rates and elevated antioxidant content (Akram *et al*. 2022, Cai *et al*. 2023). Numerous studies have examined leaf shape and physiological characteristics in native and invasive species, revealing that invasive species often exhibit a larger specific leaf area (van Kleunen *et al*. 2010), higher root and shoot growth rates (Ni *et al.* 2018), and greater antioxidant enzyme activity and antioxidant content (Suby *et al*. 2024). These morphological and physiological traits, together with their plasticity, are closely linked to invasion success across habitats, as they regulate plant growth and adaptability under varying environmental conditions (Wang *et al*. 2017a, Damián *et al*. 2020). However, few studies to date have focused on functional traits and growth differences within the same invasive species across different habitats. This evidence gap limits our understanding of how morphological and physiological plasticity varies in invasive plants under distinct environmental settings.

Higher resource competitiveness and strong tolerance to environmental stress are crucial for the successful establishment and persistence of perennial invasive species (Allred *et al*. 2010, Adams *et al*. 2023). Studies have shown that plant communities invading tropical and subtropical regions often exhibit traits such as rapid growth, high adaptability, and tolerance to high temperature and light intensity (Martin *et al*. 2009). Invasive plants characterized by rapid growth but low shade tolerance tend to exhibit greater physiological plasticity but lower morphological plasticity (Valladares *et al*. 2002). Phenotypic plasticity in morphological and physiological traits enhances the ability of invasive species to exploit limited resources, particularly under resource-constrained conditions (Steinger *et al*. 2003, Funk 2008, James *et al*. 2011, Hou *et al*. 2015). In resource-poor or stressful environments, resource conservation (*e.g*., storage and retention of existing leaves) may be more advantageous than resource acquisition (*e.g*., growth of new leaves or roots). Consequently, species adapted to such environments may exhibit reduced phenotypic plasticity (Steinger *et al*. 2003). However, individuals of the same species often show substantial variation in morphological and physiological plasticity across different habitats (Wu and Kao 2021). When responding to environmental changes, plants generally incur lower costs from physiological plasticity than from morphological plasticity, as restructuring morphological tissues demands greater energy investment (Grime and Mackey 2002).

The objective of this study was to evaluate variation in morphological and physiological plasticity of the invasive plant *Sphagneticola trilobata* (L.) Pruski under contrasting light environments and to explore how these changes relate to invasion potential. Two field habitats with contrasting light availability were established at Hanshan Normal University in Chaozhou, Guangdong Province, China, representing low-light and full-light conditions. We measured eight morphological traits and nine physiological traits of leaves to assess differences in growth performance and invasion potential of *S. trilobata* under contrasting light intensities. Specifically, this study addressed the following questions: (*1*) In which light environment does *S. trilobata* exhibit greater invasion potential? (*2*) Which morphological and physiological plasticity strategies does *S. trilobata* preferentially employ to enhance invasion success?

Materials and methods

Research location: The plant material used in this study was *S. trilobata* collected from a hillside at Hanshan Normal University in Chaozhou City, Guangdong Province, China (N 23°39', E 116°39'). The area comprised two adjacent habitats with contrasting light conditions: one with a high-density planting of trees such as *Pinus massoniana* Hort. Ex Mast. (Pinaceae), *Acacia confusa* Merrill (Fabaceae), and *Ficus microcarpa* Blume (Moraceae), creating a low-light environment; the other was an open habitat dominated by herbaceous vegetation, representing a full-light environment. These two habitats are located approximately 20 m apart. The slope of the full-light habitat plot is 14°, and its aspect is 2° west of south. The slope of the low-light habitat is 12°, and its aspect is 5° west of south. During the experiment, we used a quantum sensor to periodically measure photosynthetically active radiation (PAR) in both habitats (averaging multiple measurements taken at solar noon on clear, cloudless days). In the full-light environment, PAR averaged 1,800 ± 150 μmol(photon) m^{-2} s^{-1} (100% of ambient full sunlight). In the low-light environment, where shading was provided by the tree canopy, PAR averaged 630 ± 110 μmol(photon) m^{-2} s^{-1} (approximately 35% of ambient full sunlight). Preliminary assessments of

soil moisture content and pH in both habitats revealed no significant differences. The regional climate is a subtropical monsoon, characterized by distinct wet and dry seasons, with most rainfall occurring during the wet season (April to September). The experiment was conducted during the wet season in 2023, when the average temperature was 26°C and total rainfall ranged from 1,700 to 1,900 mm. Before the experiment, preliminary surveys of *S. trilobata* in the region were conducted. These natural populations of *S. trilobata* plants have been established in the study area for at least five years. The research team identified the two naturally occurring *S. trilobata* populations in 2022. These areas were subsequently designated as study plots and managed under uniform conditions, including regular watering, fertilization, and weeding, to minimize variation due to competition for water and nutrients. Weeding was implemented to maintain monocultures of *S. trilobata* throughout the experiment. In this study, healthy *S. trilobata* plants were randomly selected as biological replicates. At the time of sampling, two mature opposite leaves from the third stem node of each plant were collected for trait measurements. If the leaves at the third stem node failed to meet sampling criteria, alternative plants were selected to ensure that each measured trait had 15 complete biological replicates. This standardized sampling protocol ensures sample and statistical reliability.

Determination of leaf phenological and morphological traits: Fifteen healthy individuals of *S. trilobata* were selected from both full-light and low-light habitats to measure plant height, fresh mass per plant, and the diameter and length of the third stem node. Additionally, 15 fully expanded and mature leaves, each collected from a different individual of *S. trilobata*, were randomly selected to determine leaf morphological traits. The leaves were placed on a white background with a calibrated scale and sequentially labeled. They were then photographed with a camera to record phenotypic variation under different light environments. The numbered leaf images were imported into the *ImageJ* software to calculate leaf area. Subsequently, each leaf was weighed to obtain fresh mass (FM) using an analytical balance. The leaves were then oven-dried at 40°C for 4 h to remove free water, after which they were reweighed to obtain dry mass 1 (DM1). Next, they were further dried at 75°C for 72 h to remove bound water and reweighed to obtain dry mass 2 (DM2). Finally, for each leaf, the following parameters were calculated: free water content [(FM – DM1)/FM] (Singh *et al*. 2006), bound water content [(DM1 – DM2)/FM], free-to-bound water ratio, dry matter content (DM2/FM), leaf mass per area (LMA), specific leaf area (SLA), and leaf thickness [LT = 1/(SLA × LDMC)] (Vile *et al.* 2005), where LDMC denotes leaf dry matter content.

Chlorophyll content: Chlorophyll content was determined using the 80% acetone extraction method (Yu *et al*. 2023a). Healthy, fully expanded leaves from the third stem node of *S. trilobata*, grown under contrasting light environments, were collected, surface-washed with distilled water, and gently blotted dry. Each treatment (full-light and low-light habitats) comprised 15 biological replicates. Using a 6-mm diameter hole punch, two leaf discs were sampled per leaf (avoiding major veins). To ensure complete pigment extraction, the leaf discs were finely minced as much as possible and transferred to a centrifuge tube containing 1.5 mL of pre-chilled 80% acetone. Samples were incubated in the dark at 4°C for 24 h with gentle agitation every 6 h until leaf tissue was completely bleached. The absorbance of the supernatant was measured at 663, 645, and 470 nm using a *UV2450* spectrophotometer (*Shimadzu*, Tokyo, Japan). Photosynthetic pigment concentrations were calculated according to Wellburn (1994): Chl *a* [μg mL^{-1}] = 12.21A_{663} – 2.81A_{645}; Chl *b* [μg mL^{-1}] = 20.13A_{645} – 5.03A_{663}; total Chl [μg mL^{-1}] = Chl *a* + Chl *b*; Car [μg mL^{-1}] = (1,000 A_{470} – 3.27 Chl *a* – 104 Chl *b*)/198.

Antioxidant content: Healthy leaves of *S. trilobata*, grown under different light conditions, were collected, and two 6-mm-diameter leaf discs were sampled from each plant using a hole punch (avoiding major veins). The discs were immediately transferred to centrifuge tubes containing 2 mL of pre-chilled 95% methanol and extracted in the dark at 4°C for 72 h with gentle agitation every 12 h to ensure complete solubilization of antioxidant metabolites. Flavonoid content, total phenolic content, and total antioxidant capacity were then quantified, and each treatment included 15 biological replicates.

Flavonoid content was determined following a modified version of the method described by Heimler *et al*. (2005), as adapted by Yu *et al*. (2023a). A standard curve was constructed using serial dilutions of catechin, and flavonoid concentrations were calculated accordingly.

Total phenolic content was measured using a modified Folin–Ciocalteu assay based on Ainsworth and Gillespie (2007). Gallic acid was used to generate the calibration curve, and total phenolic content was calculated accordingly.

Total antioxidant capacity was assessed *via* the DPPH (2,2-diphenyl-1-picrylhydrazyl) radical scavenging assay, following the protocol of Saha *et al*. (2008) with minor modifications. A standard curve was prepared using graded concentrations of DPPH solution. The total antioxidant capacity is expressed as the DPPH radical scavenging activity.

Chlorophyll fluorescence: Chlorophyll fluorescence parameters were measured using a *PAM2500* portable modulated chlorophyll fluorometer (*Heinz Walz GmbH*, Effeltrich, Germany). Measurements were conducted on a clear, cloudless day. Healthy, fully expanded *S. trilobata* plants grown under different light conditions were selected. Fifteen mature leaves from the third stem node were randomly chosen for analysis. Prior to measurement, leaves were dark-adapted for 30 min. Initial fluorescence (F_0) was then recorded under a measuring light intensity of < 0.05 μmol(photon) m^{-2} s^{-1}. Subsequently, a saturating pulse [9,000 μmol(photon) m^{-2} s^{-1}, duration: 0.8 s] was applied to determine maximum fluorescence (F_m) and variable fluorescence (F_v). The maximum quantum yield

of PSII photochemistry (F_v/F_m) under dark-adapted conditions was calculated automatically by the instrument. Thereafter, actinic light intensity of the instrument was set to 800 μmol(photon) m^{-2} s^{-1} to measure the steady-state chlorophyll fluorescence of the leaves of *S. trilobata*. We selected 800 μmol(photon) m^{-2} s^{-1} to ensure measurements of both full-light and low-light treated *S. trilobata* under light saturation conditions, thereby enabling comparison of their optimal correlated parameters under optimal light conditions. The selection of the light intensity is based on the pre-experiment that it can ensure that the leaves of *S. trilobata* can reach the light saturation state, so as to obtain the best fluorescence parameters. At the same time, it also refers to the research of Cai *et al.* (2023). Following measurement, the instrument output the following parameters: maximum quantum yield of PSII photochemistry (F_v/F_m), the actual photochemical quantum yield of PSII $Y_{(II)}$, and electron transport rate (ETR).

Gas-exchange parameters: Photosynthetic performance of *S. trilobata* leaves under different light conditions was assessed using a *Li-6400* portable infrared gas analyzer (*LI-COR Biosciences*, Lincoln, NE, USA). Measurements were conducted on clear, cloudless days between 08:30 and 12:00 in the morning. For each light condition, 15 healthy mature leaves from the third stem node of randomly selected plants were measured. Before data collection, the instrument was powered on, calibrated with ambient air, and allowed to stabilize for at least 30 min. During measurement, standardized environmental settings were applied in the leaf chamber: photosynthetic photon flux density (PPFD) = 800 μmol m^{-2} s^{-1} (provided by a 9:1 red:blue LED array), leaf chamber temperature at 25°C, relative humidity = 60%, and CO_2 concentration = 400 μmol mol^{-1} (matching ambient atmospheric levels). This PPFD was selected based on preliminary tests confirming light saturation in both full-light and low-light acclimated leaves, thereby enabling a reliable comparison of light-saturated photosynthetic parameters, consistent with previous studies (Cai *et al*. 2023). A 10-min induction period under the same PPFD of 800 μmol m^{-2} s^{-1} preceded each measurement to ensure photosynthetic steady state. Net photosynthetic rate (P_N) was recorded only after all gas-exchange parameters stabilized.

Data analysis: Data were processed and organized using *Microsoft Excel 2016* and analyzed using *IBM SPSS Statistics 18.0* (*IBM Corp*., Armonk, NY, USA). Independent-sample *t*-tests were conducted to assess the effects of light treatment on leaf morphological traits, protective metabolite concentrations, photosynthetic performance, and chlorophyll fluorescence parameters. Figures were generated using *SigmaPlot 14.0* (*Systat Software*, San Jose, CA, USA). All data are presented as mean ± standard error (SE). Regression analyses were also performed in *SigmaPlot 14.0*. Principal component analysis (PCA) was conducted using *CANOCO 4.5* (*Microcomputer Power*, Ithaca, NY, USA). In addition, structural equation modelling (SEM) was employed to quantify the standardized total effects of explanatory variables on responses under different light conditions. Non-significant paths were removed stepwise to improve model fit. The best-fitting model was selected based on the maximum likelihood χ^2 test, root mean square error of approximation (RMSEA) index, and comparative fit index (CFI). 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

Plant leaf phenotypic traits: Phenotypic analysis of mature *S. trilobata* leaves under different light conditions revealed that low-light-grown leaves exhibited higher leaf greenness than those grown under full light (Fig. 1*A*). Furthermore, plants cultivated under full light showed significantly greater fresh mass (Fig. 1*B*), plant height (Fig. 1*C*), diameter of the third internode (Fig. 1*D*), length of the third internode (Fig. 1*E*), free water content (Fig. 1*F*), leaf mass per area (LMA) (Fig. 1*H*), leaf thickness (LT) (Fig. 1*J*), and leaf dry matter content (LDMC) (Fig. 1*K*) compared with low-light-grown counterparts. Conversely, the bound water content (Fig. 1*G*) and specific leaf area (SLA) (Fig. 1*I*) were significantly lower under full light.

Physiological traits in plant leaves: Photosynthetic pigment analysis showed that Chl *a* content (Fig. 2*A*), Chl *b* content (Fig. 2*B*), total Chl content (Fig. 2*C*), Chl *a*/*b* ratio (Fig. 2*D*), and carotenoid content (Fig. 2*M*) were significantly lower in *S. trilobata* grown under full light than in plants grown under low-light conditions. In contrast, the carotenoid-to-total-chlorophyll ratio (Fig. 2*E*) was significantly higher under full light. Leaf antioxidant metabolites profiling showed that flavonoid content (Fig. 2*F*), total phenolic content (Fig. 2*G*), and total antioxidant capacity (Fig. 2*H*) were significantly greater in full-light-grown mature leaves than in low-light-grown counterparts. Similarly, chlorophyll fluorescence and gas-exchange parameters indicated significantly higher F_v/F_m (Fig. 2*I*), $Y_{(II)}$ (Fig. 2*J*), ETR (Fig. 2*K*), and P_N (Fig. 2*L*) under full light.

Correlation analysis of plant fresh mass and plant height with leaf morphological traits: Correlation analyses were performed to examine relationships between fresh mass, plant height, and leaf traits, including free water content, bound water content, LMA, SLA, LDMC, and LT. The results indicated that fresh mass was significantly negatively correlated with bound water and SLA (Fig. 3*B*,*D*), and positively correlated with LMA, LDMC, and LT (Fig. 3*C*,*E*,*F*). Similarly, plant height was significantly negatively correlated with bound water and SLA (Fig. 3*H*,*J*), and positively correlated with LMA and LDMC (Fig. 3*I*,*K*), but showed no significant correlation with free water content (Fig. 3*G*) or LT (Fig. 3*L*).

Correlation analysis between plant fresh mass and plant height with leaf physiological traits: *Pearson*'s correlation analyses were conducted to examine relationships between plant growth traits (fresh mass

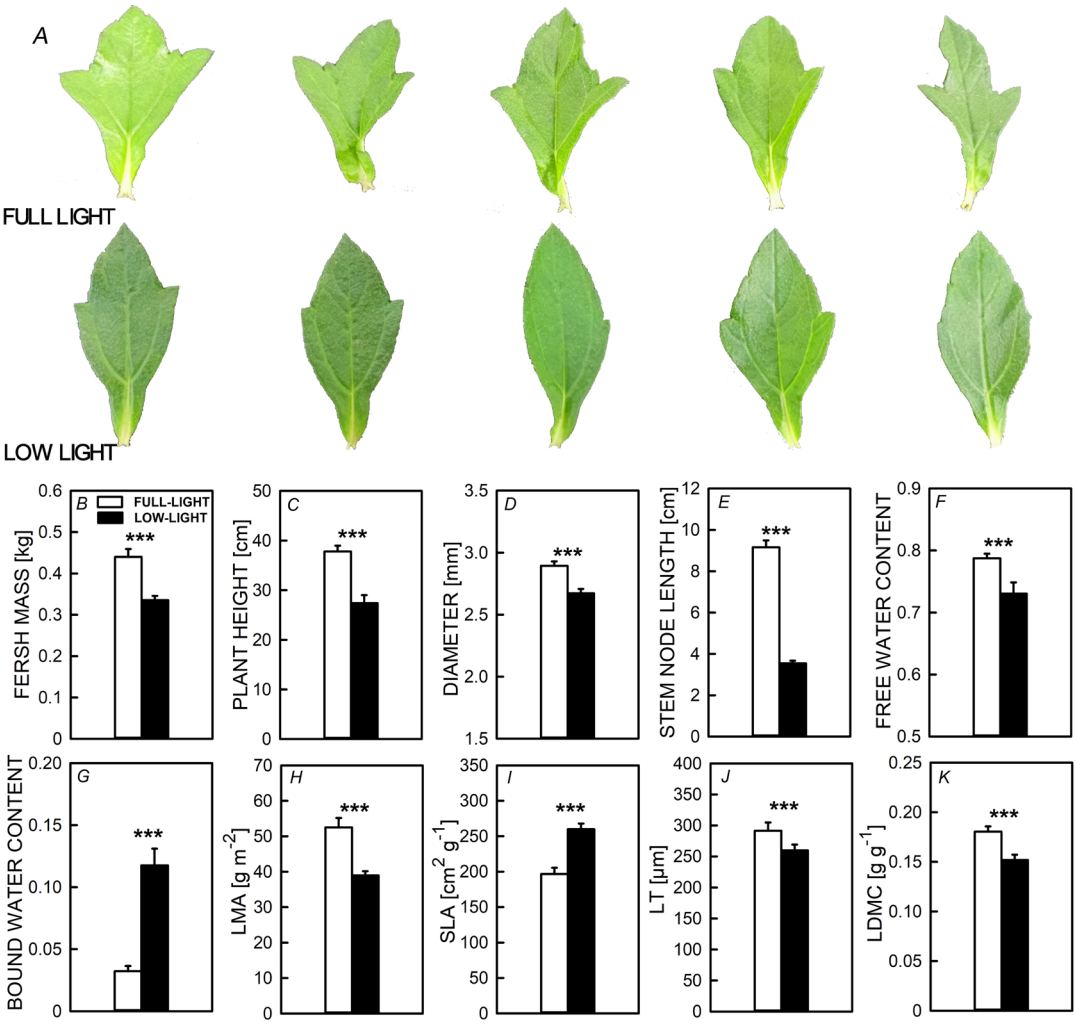

Fig. 1. Changes in phenotypic traits of the invasive plant *Sphagneticola trilobata* leaves under different light environments. Leaf phenotypes (*A*), fresh mass per plant (*B*), plant height per plant (*C*), diameter of the third internode (*D*), length of the third internode (*E*), free water content (*F*), bound water content (*G*), leaf mass per area (LMA) (*H*), specific leaf area (SLA) (*I*), leaf thickness (LT) (*J*), and leaf dry matter content (LDMC) (*K*). * indicates significant difference at the 0.05 level; ** indicates significant difference at the 0.01 level; *** indicates significant difference at the 0.001 level.

and plant height) and leaf physiological traits in *S. trilobata*. Fresh mass and plant height exhibited consistent correlation patterns with leaf physiological traits. Neither trait was significantly correlated with F_v/F_m (Fig. 4*A*,*F*). In contrast, both fresh mass and plant height were significantly positively correlated with the carotenoid-to-total-chlorophyll ratio, flavonoid content, total phenolic content, total antioxidant capacity, ETR, $Y_{(II)}$, and P_N (Fig. 4*B-E*,*G-J*,*L-N*,*P-R*), and were significantly negatively correlated with Chl (*a*+*b*) (Fig. 4*K*,*O*). Furthermore, *Pearson*'s correlation analysis across all leaf morphological and physiological traits showed that, except for bound water content, SLA, and chlorophyll content, most morphological traits were positively associated with physiological traits (Fig. 5).

Principal component analysis and structural equation modeling of morphological and physiological traits in *S. trilobata*: Principal component analysis (PCA) was performed on leaf functional and physiological traits of leaves of *S. trilobata* grown under different light conditions, and two principal components were extracted, with principal component 1 (PC1) explaining 59.9% of the variation in traits and principal component 2 (PC2) explaining 13.5% of the variation in traits. PC1 was predominantly loaded by growth-related traits (fresh mass, plant height, LMA, LT, LDMC), photosynthetic traits (P_N, ETR, $Y_{(II)}$), and photoprotective metabolite traits (phenolics, flavonoids, total antioxidant capacity, Car/Chl), *etc*. (Fig. 6*A*). Thus, PC1 represents an integrated axis of variation in growth performance, photosynthetic capacity, and photoprotection. Additionally, results showed that *S. trilobata* grown under full-light conditions mainly clustered in the left axis direction of PC1, while those grown under low-light conditions mainly clustered in the right axis direction of PC1 (Fig. 6*B*). Structural equation modeling (SEM) was used to evaluate the effects of light conditions on morphological traits, physiological traits, and growth

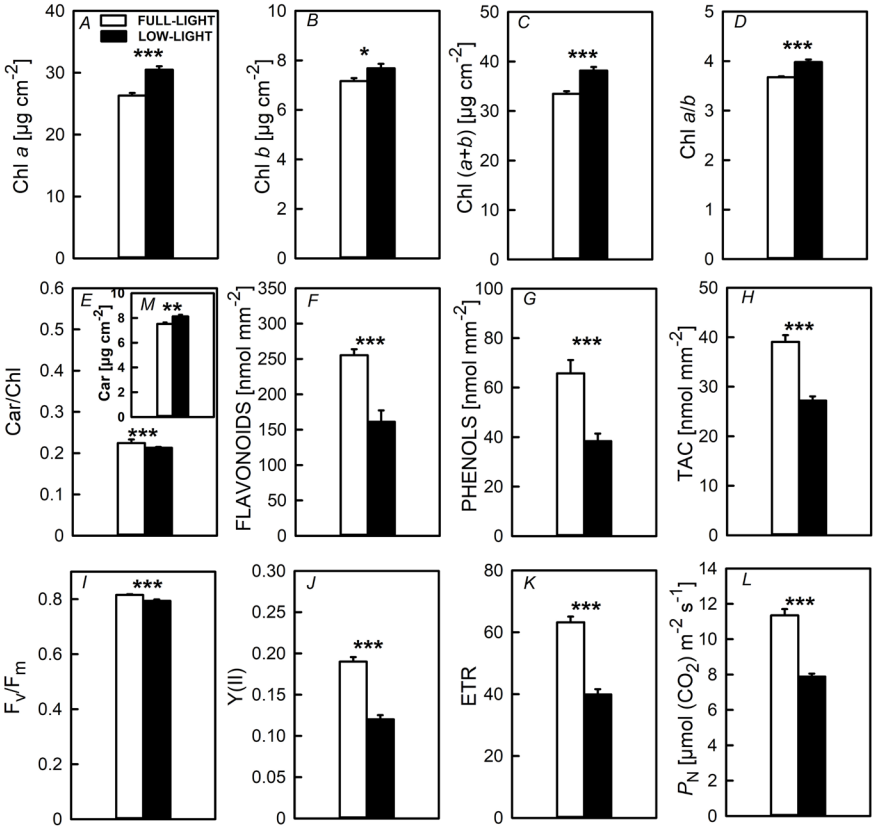

Fig. 2. Changes in photosynthetic pigments, leaf photoprotective metabolites, chlorophyll fluorescence parameters, and photosynthetic rate of *Sphagneticola trilobata* leaves under different light environments. Leaf photosynthetic pigments include: chlorophyll *a* (Chl *a*) (*A*), chlorophyll *b* (Chl *b*) (*B*), total chlorophyll (Chl *a*+*b*) (*C*), chlorophyll *a*/*b* (Chl *a*/*b*) (*D*), carotenoids (Car) (*M*), and carotenoids to total chlorophyll ratio (Car/Chl) (*E*). Leaf antioxidant metabolites include: flavonoids (*F*), phenols (*G*), and total antioxidant capacity (TAC) (*H*). The chlorophyll fluorescence parameters include: maximum quantum yield of PSII photochemistry (F_v/F_m) (*I*), actual photochemical efficiency of PSII ($Y_{(II)}$) (*J*), electron transfer rate (ETR) (*K*), maximum net photosynthetic rate (P_N) (*L*). * indicates significant difference at the 0.05 level; ** indicates significant difference at the 0.01 level; *** indicates significant difference at the 0.001 level.

performance. The transition from low-light to full-light conditions had significant positive effects on antioxidant physiology (PC1: 0.88), morphological plasticity (PC1: 0.65), photosynthetic physiology (PC1: 0.92), F_v/F_m (0.57), and biomass (PC1: 0.78), but a significant negative effect on morphological plasticity 2 (PC1: –0.37) (Fig. 6*C*). Standardized total effects indicated that five of the six SEM factors (antioxidant physiology PC1, morphological plasticity 1 PC1, photosynthetic physiology PC1, F_v/F_m, and biomass PC1) were positively influenced by light conditions, whereas one factor (morphological plasticity 2 PC1) showed a negative response (Fig. 6*D*).

Discussion

This study demonstrates that the invasive plant *S. trilobata* exhibits significant differences in growth across populations from different light environments, accompanied by corresponding changes in morphological and physiological traits. We confirmed that *S. trilobata* exhibits greater invasive potential under full-light environments, and this enhanced potential is primarily mediated by physiological plasticity, with morphological plasticity playing a complementary role.

Growth differences of invasive plants under different light environments: Differences in environmental conditions across heterogeneous habitats influence the growth and resource allocation strategies of invasive plants (van Kleunen *et al.* 2010, Xiong *et al.* 2024). Compared to native plants, invasive species often adopt a low-cost, high-return investment strategy (Nagel and Griffin 2001, Song *et al.* 2007, Hou *et al.* 2015). However, few studies have examined whether resource allocation patterns within the same invasive species vary across habitats, despite the importance of such variation for identifying environments that favor invasion success. Once established, invasive plants can negatively impact ecosystems by competitively displacing native species, altering soil microbial communities, reducing biodiversity, and disrupting carbon and nitrogen cycles (Andreu and Vilà 2010). Therefore, understanding the adaptive strategies of invasive plants across different habitats is critical for predicting and mitigating their ecological impacts.

In this study, *S. trilobata* exhibited superior growth performance under full-light conditions, with significantly higher growth rates and biomass accumulation than under low-light conditions (Fig. 1). This is consistent with

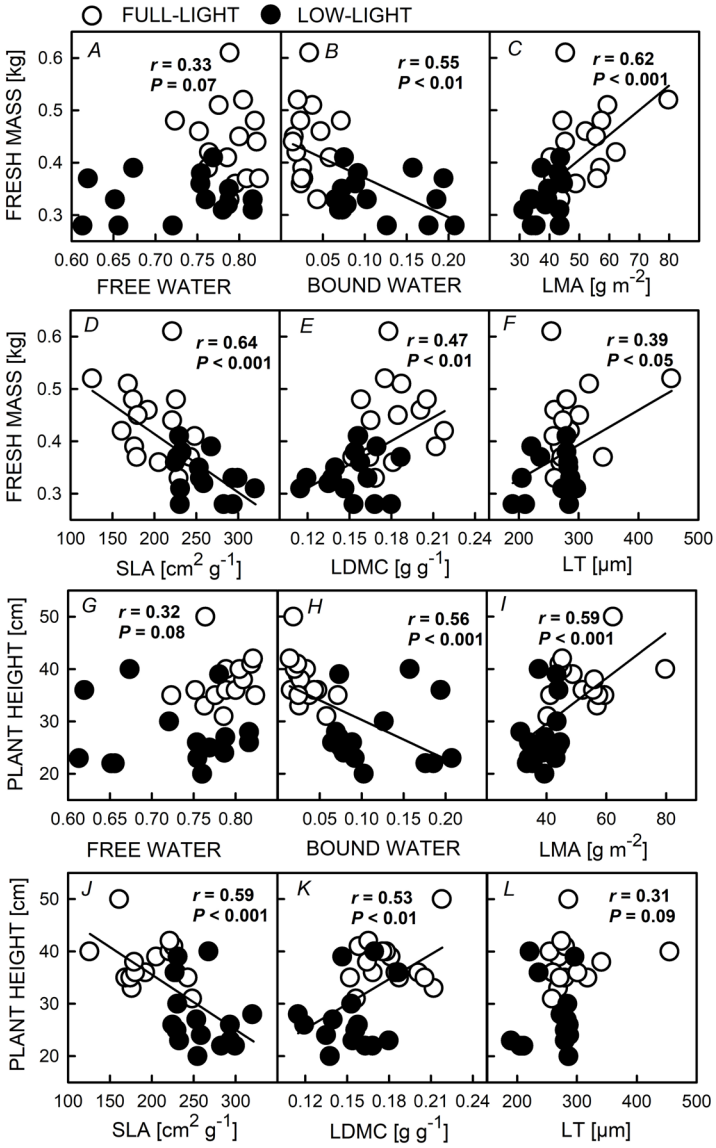

Fig. 3. The correlation between the fresh mass per plant and leaf functional traits of *Sphagneticola trilobata* under different light environments (*A–F*), as well as the correlation between plant height per plant and leaf functional traits (*G–L*). Leaf mass per area (LMA), specific leaf area (SLA), leaf dry matter content (LDMC), and leaf thickness (LT).

previous research showing that low-light environments significantly limit plant growth (Hou *et al*. 2015). Stem length and diameter at the third node of *S. trilobata* were significantly lower under low-light environments than under full light. On the one hand, this reflects the constraints imposed by light availability on stem growth, consistent with biomass patterns. On the other hand, it suggests that plants may optimize resource allocation by reducing stem investment, demonstrating a trade-off between vegetative growth and structure support. This capacity for rapid adjustment enables them to maintain a competitive advantage under variable light conditions, thereby intensifying competitive displacement of native plant communities (Kuebbing and Nuñez 2016). Additionally, the physiological characteristics of invasive plants often differ due to different growth habitat types (Claridge and Franklin 2002). Invasive species can gain a competitive advantage in environments with fluctuating resource availability, facilitating their spread and leading to simplified community structure and reduced ecosystem stability (Kuebbing and Nuñez 2016). This study further demonstrates that *S. trilobata* adapts to light variability through coordinated morphological and physiological adjustments. Morphological and physiological plasticity are key determinants of invasiveness and represent two crucial strategies for plant adaptation to environmental change (Zunzunegui *et al*. 2009, Hahn *et al*. 2012). These forms of plasticity do not operate independently but interact to regulate plant responses to environmental gradients (Wang *et al.* 2006), collectively shaping invasive potential. However, they differ in their hierarchical roles during invasion, response speed, and resource costs. Morphological adjustments provide the structural foundation for resource acquisition. Under resource-constrained conditions, morphological plasticity may respond first (Moczek *et al*. 2011), supporting basic survival through structural adaptation (Sun *et al*. 2023, Wang *et al*. 2025). Physiological regulation governs resource-use efficiency and metabolic output. Under resource-rich conditions, physiological plasticity becomes the primary

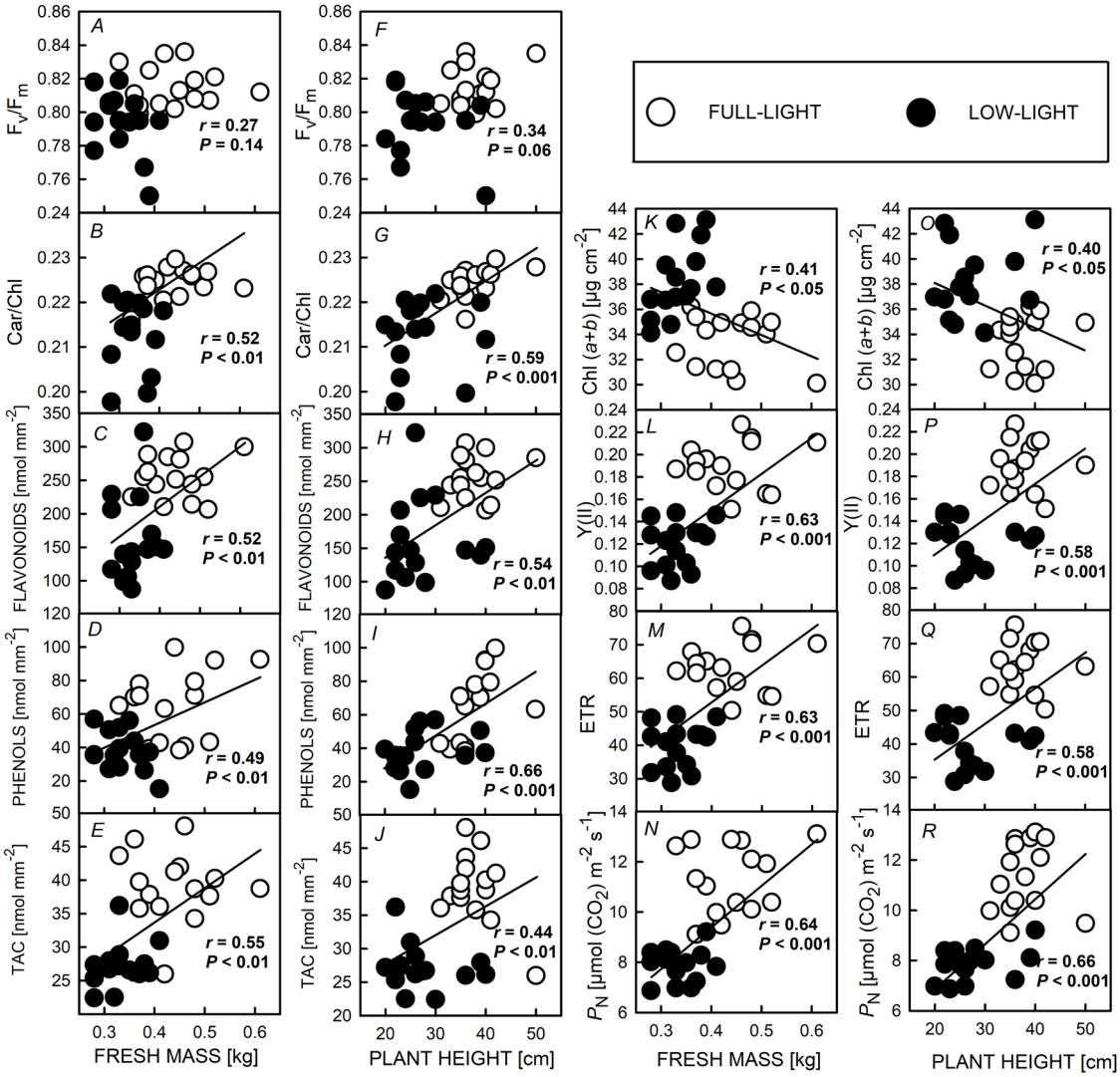

Fig. 4. The correlation between the fresh mass per plant of invasive plant *Sphagneticola trilobata* and photoprotective metabolites and photosynthetic capacity under different light environments (*A–E*, *K–N*), as well as the correlation between plant height per plant and photoprotective metabolites and photosynthetic capacity (*F–J*, *O–R*).

driver of rapid growth and competitive dominance (Funk *et al*. 2008, Mou *et al*. 2013), whereas the morphological plasticity plays a complementary and reinforcing role. This functional differentiation ultimately determines the competitive capacity and expansion potential of invasive plants across heterogeneous environments.

Morphological plasticity of invasive plants under different light environments and its relationship with growth: The successful colonization and expansion of invasive plants typically depend on their plastic responses to heterogeneous environments (Sharma *et al*. 2024). To cope with low-light conditions, *S. trilobata* compensates for energy limitations by enhancing its light-capture efficiency through characteristics such as increased SLA and chlorophyll content (Fig. 1*A*,*I*; Fig. 2*A-D*,*M*), which is consistent with previous findings (Zhang *et al*. 2007, Huang *et al*. 2011). However, notably, *S. trilobata* exhibited greater morphological plasticity and stronger growth advantages under full-light conditions. Specifically, plants grown under full-light conditions showed higher free water content, LMA, LT, and LDMC. Among these, the elevated free water content may reflect a more active metabolic state and heightened physiological activity (Huang *et al*. 2020); in contrast, increased LMA, LT, and LDMC indicate denser leaf anatomy and enhanced structural investment (Ordonez *et al*. 2010). Morphological plasticity is primarily expressed through adjustments in resource-acquisition structures (Grams and Andersen 2007). Under low-light conditions, plants maximize light interception by increasing SLA and chlorophyll content, a classic example of survival-oriented plasticity. Although this strategy supports persistence, it is insufficient to sustain rapid growth. Under full-light conditions, light-driven developmental responses promote increases in LT, LDMC, and stem biomass allocation, resulting in a more robust and resource-efficient structural phenotype. This expansion-oriented plasticity directly facilitates

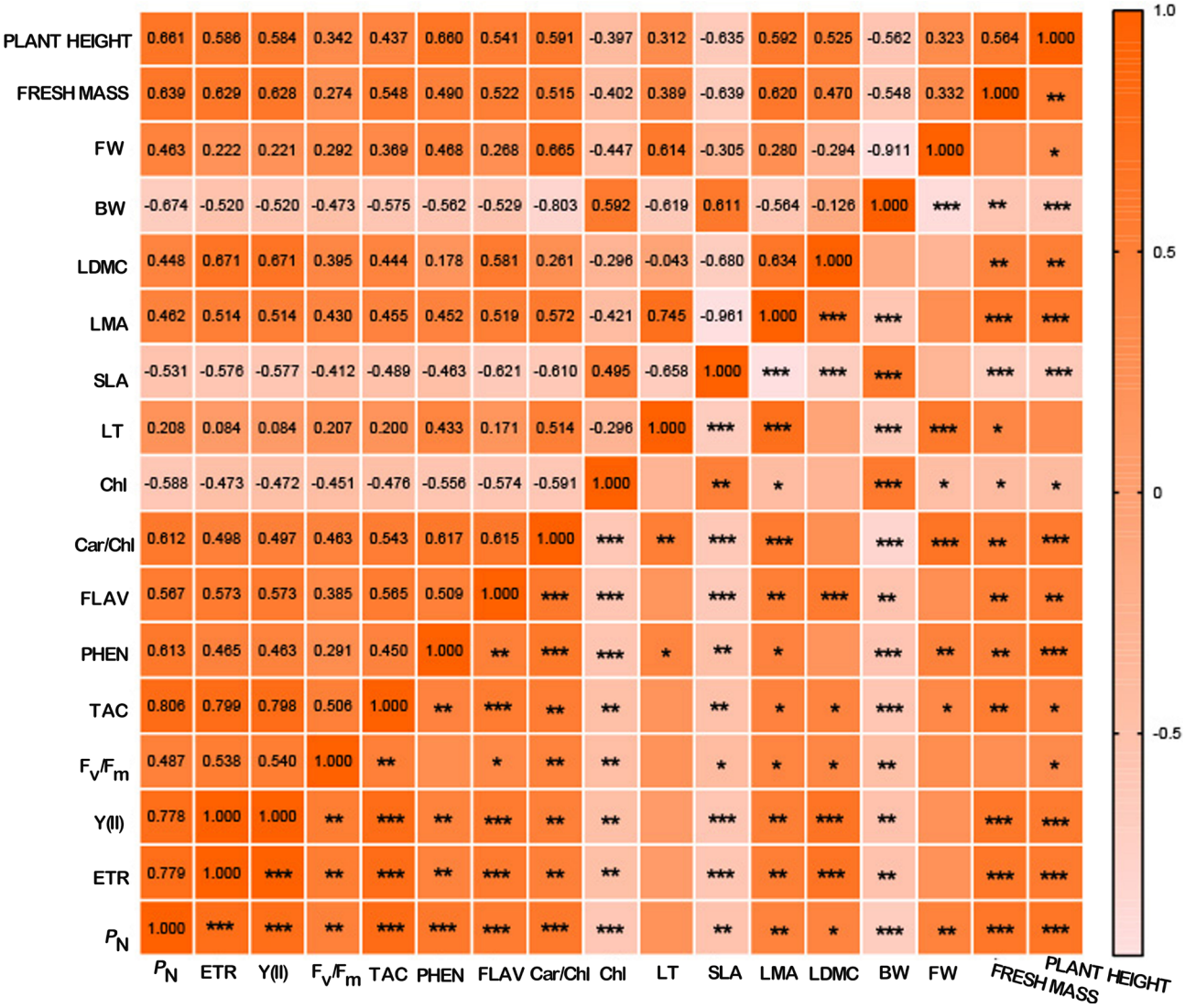

Fig. 5. *Pearson* correlation coefficients of 8 morphological traits and 9 physiological traits of the invasive plant *Sphagneticola trilobata* leaves under different light environments. Significant correlations are indicated in bold (**P*<0.05; ***P*<0.01; ****P*<0.001). FLAV – flavonoids, PHEN – phenolics, TAC – total antioxidant capacity, FW – free water content, BW – bound water content, Chl – chlorophyll, Car/Chl – carotenoids/total chlorophyll.

high biomass accumulation and competitive dominance. Such context-dependent shifts in morphological strategy highlight the ability of invasive plants to optimize resource allocation under varying resource availability. These morphological changes are highly consistent with physiological indicators of enhanced photosynthetic capacity (Fig. 5).

Research confirms that invasive plants exhibit different levels of morphological plasticity in various environments (Bernado *et al*. 2021). Such variation is closely associated with their invasion capacity (Jardeleza *et al*. 2022). This is because some invasive plants possess inherently superior competitive ability, enabling them to gain systemic advantages in highly competitive environments (Callaway and Aschehoug 2000). Our correlation analysis revealed strong associations among leaf morphological traits along the light-intensity gradient (Fig. 5). However, the relationship between morphological traits and growth in the invasive plant *S. trilobata* appears more complex. While most morphological traits showed significant positive correlations with growth and biomass, certain traits, including bound water content and SLA, showed negative correlations (Fig. 3). This pattern suggests that *S. trilobata* employs a coordinated yet selective morphological adjustment strategy in response to light availability, optimizing adaptation specifically under full-light conditions. Therefore, based on morphological plasticity results, this study tentatively indicates that the higher invasiveness of *S. trilobata* under full-light conditions is linked to its morphological plasticity, but these effects may partially counteract one another. This inference is further supported by structural equation modeling (Fig. 6*C*,*D*). *S. trilobata* is an invasive plant with strong clonal (asexual) reproductive capacity, and

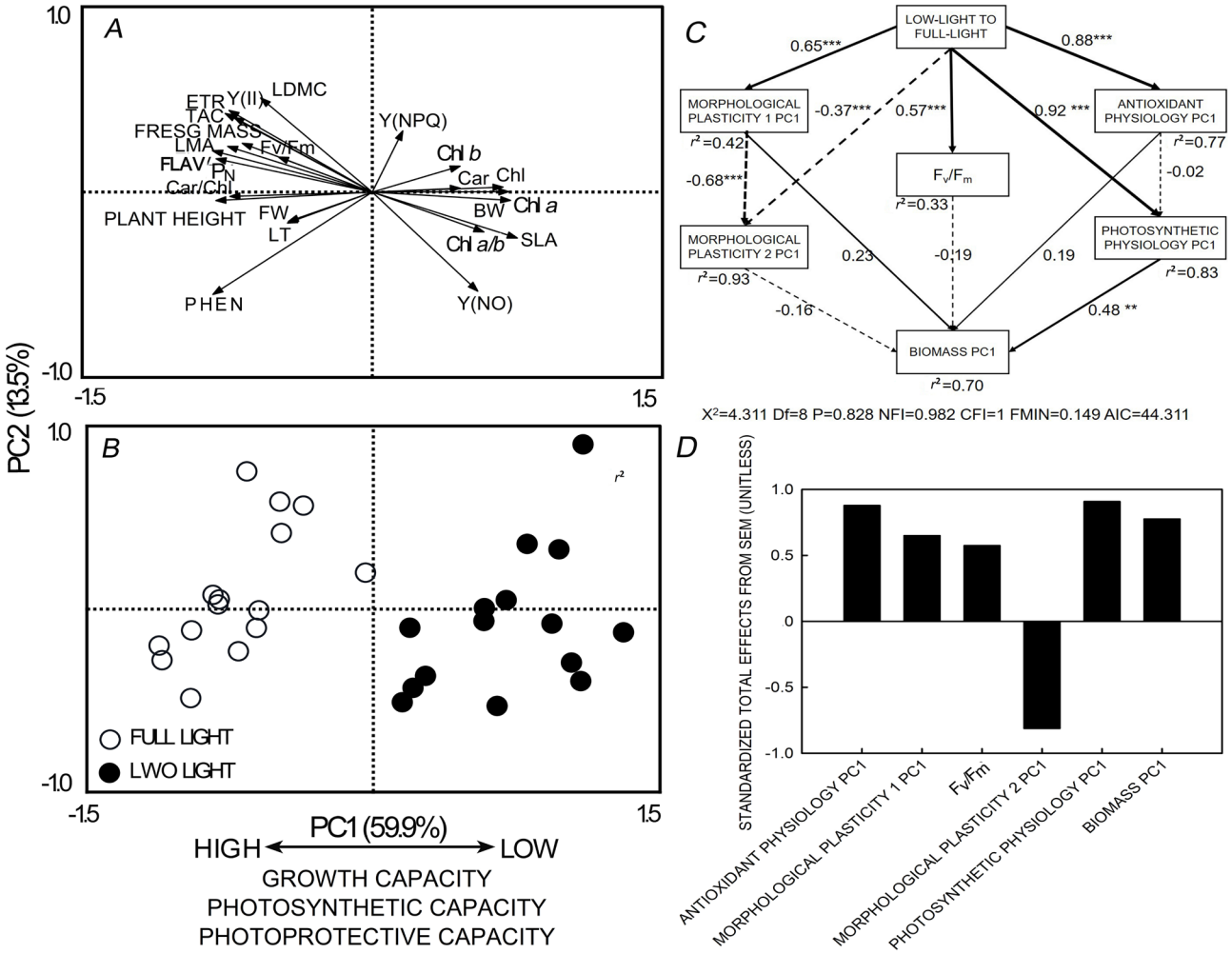

Fig. 6. Principal component analysis of 8 morphological traits and 9 physiological traits of *Sphagneticola trilobata* leaves under different light environments (*A*,*B*). The structural equation models (SEM) of physiological and morphological indices of *S. trilobata* under low light to full light (*C*,*D*). The different factors showed direct and indirect effects (*C*) and standardized total effects (*D*) on the growth of *S. trilobata*. Antioxidant physiology PC1: principal component 1 extracted from Flav, Phen, TAC, and Car/Chl; Morphological plasticity1 PC1: principal component 1 extracted from FW, LDMC, LMA, and LT; Morphological plasticity2 PC1: principal component 1 extracted from BW and SLA; Photosynthetic physiology PC1: principal component 1 extracted from $Y_{(II)}$, ETR, and P_N; Biomass PC1: principal component 1 extracted from fresh mass and plant height. 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 thickness of the arrow represents the magnitude of the path coefficients. The numbers adjacent to boxes of response variables denote the explained variance (R^2). * indicates significant difference at 0.05 level. ** indicates significant difference at 0.01 level. *** indicates significant difference at the 0.001 level. $Y_{(NPQ)}$ – the quantum yield of regulatory energy dissipation at PSII; $Y_{(NO)}$ – the quantum yield of unregulated energy dissipation at PSII.

branching ability is a key morphological indicator of its growth and expansion potential. Previous studies have shown that invasive alien plants can attain significant survival and competitive advantages in heterogeneous environments through clonal reproduction (Wang *et al.* 2017b, Chen *et al.* 2019). However, this study primarily focuses on leaf morphological responses to light gradients and has not yet systematically examined clonal-growth-related traits, such as branching ability, in the invasion process. Future research should integrate clonal reproductive characteristics to achieve a more comprehensive understanding of *S. trilobata*'s invasion mechanisms under different light conditions.

Physiological plasticity of invasive plants under different light environments and its relationship with growth: Invasive species generally exhibit high physiological plasticity, a trait considered key to their adaptation to heterogeneous environments (Davidson *et al.* 2011, Luo *et al.* 2017). This study showed that although *S. trilobata* exhibited measurable morphological plasticity in different light habitats (Figs. 1 and 2), its physiological plasticity played a more dominant role in regulating growth performance. This finding suggests that invasive plants can achieve efficient resource use at relatively low cost through rapid physiological adjustments, in contrast to the slower and structurally constrained nature

of morphological changes (Grime and Mackey 2002, Hou *et al*. 2015). Consistently, growth and biomass of *S. trilobata* in different light environments showed significant positive correlations with nearly all measured physiological and morphological factors except chlorophyll content (Figs. 4 and 5). This pattern indicates that enhanced physiological capacity facilitates more efficient resource exploitation and greater tolerance to abiotic stress, thereby promoting invasion success. Changes in the abundance of physiological metabolites and the degree of functional matching with the environment are crucial for sustaining optimal growth performance, including shifts in antioxidant contents, heat dissipation capacity, and photosynthetic efficiency, which commonly occur under fluctuating environmental conditions (Yu *et al*. 2021, 2023b).

S. trilobata exhibited faster biomass accumulation under full-light conditions, driven by light-regulated physiological adjustments, including elevated Car/Chl ratios, flavonoid and phenolic content, $Y_{(II)}$, ETR, and P_N (Fig. 2*E-L*). Enhanced heat dissipation and antioxidant capacities reflect the plant's robust photoprotective ability, safeguarding the photosynthetic apparatus from photodamage (Yu *et al*. 2023a), which is corroborated by the stable or only slightly reduced F_v/F_m values under high light (Fig. 2*I*). The higher photosynthetic capacity supports the synthesis of growth-essential metabolites (Chen *et al*. 2015, He *et al*. 2018), consistent with significantly greater LT and LDMC under full light than under low-light conditions (Fig. 1*J*,*K*). These coordinated physiological responses enable *S. trilobata* to sustain rapid growth under full-light conditions and explain its superior growth performance in high-light *vs*. low-light environments. In addition, PCA and SEM confirmed that *S. trilobata* exhibits stronger growth, enhanced photoprotection, and higher photosynthetic capacity under full-light conditions compared with low-light conditions (Fig. 6). These results highlight the critical role of leaf-level physiological traits in shaping plant responses to environmental variation, with high biomass production under full light driven by integrated regulation across multiple physiological processes. Thus, physiological trait measurements further support the conclusion that the invasiveness of *S. trilobata* is significantly greater under full-light conditions than under low-light conditions. Under full-light conditions, the synergy between high physiological plasticity and abundant resources maximizes its invasion performance. This ecological advantage is also rooted in its native origin and inherent growth strategy: *S. trilobata* is native to South America and is a naturally heliophilous species (Cai *et al*. 2021), endowed with high CO_2 fixation capacity, a broad tolerance to photosynthetically active radiation, and high quantum efficiency (Song *et al*. 2010, Li *et al*. 2016).

Conclusion: This study highlights the critical links among physiological and morphological traits and biomass accumulation in invasive plants under different light environments, demonstrating that invasive plants can expand their functional ecological niches through coordinated adjustments in both morphological and physiological plasticity, thereby enabling rapid growth. However, physiological plasticity plays a more central role than morphological plasticity in driving growth differences. Under full-light conditions, *S. trilobata* exhibits higher net photosynthetic rates, enhanced photoprotective capacity, and improved PSII operational efficiency. These physiological advantages enable the rapid conversion of abundant light resources into carbon assimilates that support growth, thereby driving superior performance. Notably, physiological responses are typically faster and less resource-intensive than morphological adjustments, allowing invasive plants to gain a competitive advantage under fluctuating environmental conditions. These findings challenge the traditional view that invasion success is governed by static traits and instead highlight the dynamic and context-dependent nature of invasion strategies. The study advances our understanding of *S. trilobata*'s competitive advantage and invasion mechanisms by quantifying the relative contributions of physiological *vs*. morphological plasticity to invasion success under different light conditions. As a clonal species, *S. trilobata* relies heavily on branching capacity, a key morphological determinant of its expansion potential, where the number and vigor of clonal ramets strongly correlate with invasive success. Future studies will employ controlled pot experiments and comparative analyses involving co-occurring native species and congeneric *Sphagneticola* species. These studies will investigate branch-specific traits, including branch strength, branch angle, and cloning integration efficiency, to clarify how branching architecture contributes to invasion success under different light gradients.

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