Research Article

Photosynthetic physiological and ecological responses of the invasive *Sphagneticola trilobata* and the native *Sphagneticola calendulacea* to experimental shading

Jun-jie Zhang1,2, Ming-ling Cai1,2, Li-hua Chen1, Xiao-hua Lin1, Jin-di Peng1, Jun-dong Huang1, Ling Shao2 and Chang-lian Peng1,*

1Guangzhou Key Laboratory of Subtropical Biodiversity and Biomonitoring, Guangdong Provincial Key Laboratory of Biotechnology for Plant Development, College of Life Sciences, South China Normal University, Guangzhou 510631, China
2College of Life Science, Zhao Qing University, Zhaoqing, Guangdong, China

#These authors contributed equally to this work
*Corresponding author
E-mail: pengchl@scib.ac.cn

Abstract

Affected by global climate change and human activities, biological invasion has become a serious global problem that not only occurs in cities and wastelands but also in forests, severely endangering biodiversity. *Sphagneticola trilobata* (L.) Pruski, 1996, is a common invasive plant in South China that can adapt to high light and high temperature environments, but its photosynthetic physiological response to shaded environments, such as forest margins, remains unclear. This study investigates the photosynthetic physiology and oxidative damage of *S. trilobata* and the native species *Sphagneticola calendulacea* (L.) Pruski, 1996, in a low-irradiance environment. The results show that, compared with the full-light group, photosynthetic gas exchange parameters (including net photosynthetic rate, stomatal conductance and transpiration rate) and chlorophyll fluorescence parameters (maximal quantum yield and actual quantum yield of PSII) of plants in the low-light group significantly decreased after shading, while intercellular CO2 and nonphotochemical quenching increased; of note, *S. trilobata* experienced smaller changes. The malonaldehyde content of *S. calendulacea* increased, while phenols and the total antioxidant capacity of *S. trilobata* declined more significantly than those of the native species tested. These results further indicate that, compared with *S. calendulacea*, *S. trilobata* exhibited a lower loss in photosynthesis and less oxidative damage under shading. This may explain why *S. trilobata* tends to spread to forests in South China.

Key words: invasion, photosynthesis, chlorophyll fluorescence parameters, oxidative damage, shade

Introduction

Climate change caused by increased human activity and globalization has exacerbated biological invasion over time (Paini et al. 2016; Horvitz et al. 2017). Biological invasion is the spread of native species to and throughout non-native areas as a result of competitive advantages afforded by the absence of otherwise natural obstacles, such that the invading species dominantly populate these new areas (Valéry et al. 2008), seriously
undermine biodiversity, and hinder the normal function of ecosystems, resulting in significant economic losses (Vilà et al. 2011). Light is one of the necessary resources for plants and they use light to maintain their lives through photosynthesis. Alien plant invasion, a specific kind of biological invasion, occurs not only in urban green areas and wilderness but also in environments that lack of light resources, such as forest edges and understories (Chmura and Sierka 2006; Tan et al. 2012).

However, different types of plants have different requirements and adaptability to light, and each species can regulate, to some extent, their morphology and physiological functions to adapt to different levels of light in their environments (Franklin 2008). External light intensities lower than normal conditions can result in modifications to the photosynthetic process, which are generally assessed by indices including photosynthetic pigment content, photosynthetic gas exchange parameters and chlorophyll fluorescence. Photosynthetic pigment is the material basis for plant photosynthesis, and the chlorophyll \( a+b \) content and chlorophyll \( a/b \) ratio decrease in plant leaves under long-term shading (Mu et al. 2010). The physiological and ecological characteristics of plant photosynthesis in different light environments can be assessed by photosynthetic parameters (Nedbal et al. 2000; Yokoya et al. 2006). Shading significantly decreases the net photosynthetic rate (\( P_n \)) of plant leaves (Dong et al. 2019), and stomatal conductance (\( G_s \)) gradually decreases, while intercellular \( CO_2 \) concentration (\( C_i \)) increases, with increased shading time and intensity (Yang et al. 2020). Chlorophyll fluorescence parameters like the maximal quantum yield of photosystem II (PSII) (\( F_{v}/F_{m} \)), the actual quantum yield of PSII (\( \Phi_{PSII} \)) and the nonphotochemical quenching (NPQ) are indicators that sensitively reflect the absorption-transmission-dissipation-distribution of light energy in the photosystem during photosynthesis (Genty et al. 1989; Schreiber et al. 1995), thereby showing the adaptation of plants to their external environments. While shading stress can cause a drop in photochemical quenching (\( qP \)) and \( \Phi_{PSII} \) and a rise in NPQ, meaning absorbed light energy flux to photosynthesis reduces and converts into nonphotochemical quenching such as heat energy (Yao et al. 2017).

The reduction in photosynthesis under shading is not only due to PSII malfunction caused by factors like decreased chlorophyll content but is also closely related to excessive accumulation of reactive oxygen species (ROS). Although ROS is well known to accumulate in plants under high irradiance, Ding et al. (2012) have shown that shading also causes ROS accumulation; in a low-light environment, excessive closure of stomata decreases \( CO_2 \) absorption, thereby limiting regeneration of \( NADP^+ \) in the Calvin cycle. Thus, a drop in \( NADP^+ \) decreases the usage of light energy received from low-light environments such that surplus light energy and an increase in the photosynthetic electron transport branch reaction finally lead to ROS generation and accumulation (Yu et al. 2021). When the
balance between ROS and the antioxidant system is broken, lipid peroxidation of cell membranes occurs (Jaleel et al. 2009), damaging the membranes. Consequently, the content of malondialdehyde (MDA), the product of membrane peroxidation, can reflect the degree of injury (Ayala et al. 2014). To alleviate ROS damage to plants, emergency mechanisms, such as nonenzyme antioxidant systems including flavonoids and total phenols, are activated and play a key role in stress tolerance (Wahid et al. 2007). Flavonoids can be oxidized by peroxidase and works in $H_2O_2$-scavenging while phenols can scavenge ROS directly (Sarker and Oba 2018).

Listed in the 100 of the World’s Worst Invasive Alien Species (Lowe et al. 2000), *Sphagneticola trilobata* (L.) Pruski, 1996, is a perennial herb of the Asteraceae family originating from tropical regions of South and Central America, which was introduced in 1970’s as a groundcover and escaped into the wild, mainly occurs at urban green areas and wilderness in present, becoming a troublesome weed in South China (Wu et al. 2004, 2012). Compared with native species in the same genus, *Sphagneticola calendulacea* (L.) Pruski, 1996, *S. trilobata* is highly adaptable to environmental changes and, due to its strong reproductive ability, can easily form monodominant populations after invading a new habitat. Once its cover exceeds 10%, it decreases plant community diversity (Qi et al. 2014). Studies have shown that *S. trilobata* has a larger leaf area and biomass, stronger photosynthetic capacity (Cai et al. 2020b) and greater tolerance against high irradiance stress, heat stress and cold stress than native species (Song et al. 2009a; Cai et al. 2020a, 2021). Several recent studies report that *S. trilobata* has a tendency to spread to forests in South China (Cao et al. 2007; Song et al. 2009b), but the mechanism by which *S. trilobata* protects itself against shading in low-light environments, such as forest edges, is still not clear. Li et al. (2016) studied changes in morphology, relative growth rate and photosynthesis of *S. trilobata*, *S. calendulacea* and their natural hybrids; however, the physiology, particularly the responses of photosynthetic physiology and oxidative stress under shading remain unknown. Therefore, we have compared *S. trilobata* and *S. calendulacea* in terms of photosynthetic physiology, chlorophyll fluorescence and antioxidants under shading to obtain a more comprehensive understanding of their responses and ecological adaptability to low-light environments. This study provides a theoretical basis for the responses of *S. trilobata* against low-light stress and enables predictions of potential areas of invasion.

**Materials and methods**

**Materials and experimental design**

*Sphagneticola trilobata* and *S. calendulacea*, grew under full sunlight, and were collected from a botanical garden in the School of Life Science (Figure 1), South China Normal University (23°08′N; 113°20′E). Five defoliated stems
of each *Sphagneticola* species were trimmed into 20 pieces (for each species) with two internodes, about 10 cm in length, with asextual propagation conducted in a thermostat with a light intensity of 100–200 μmol m$^{-2}$ s$^{-1}$ and 28 °C/25 °C day/night. After 4 weeks of rooting, uniform cuttings of two species, having 4 pairs of leaves and stem lengths reaching 15 cm, were transplanted into pots for treatment, one plant per pot and 20 pots for each species.

To study the responses of the two *Sphagneticola* species under shading, two light intensities, full sunlight and low light (30% full light) provided by a two-layer black shade cloth covered at a height of 2 m above the ground, were applied for 15 days, 5 pots per treatment per species, in January 2020. Leaves at the second to fourth leaf positions were used as experimental samples, and five repeats of each species were selected from different light intensities.
Measurement of photosynthetic pigment content

Samples (0.025 g) were collected at the end of the treatment to determine photosynthetic pigment content. Samples were frozen in liquid nitrogen, crushed into powder, and soaked in 80% acetone for 12 hours. After centrifugation, the supernatants were analyzed by spectrophotometry (UV-2450, Shimadzu, Kyoto, Japan) at 663 and 646 nm. Chlorophyll $a$ (Chl $a$), Chlorophyll $b$ (Chl $b$) and Chlorophyll $a+b$ (Chl $a+b$) sample contents were calculated using the methodology of Lichtenthaler and Buschmann (2001).

Assay of photosynthetic gas exchange parameters and chlorophyll fluorescence parameters

Photosynthetic gas exchange parameters, including net photosynthetic rate ($P_{n}$), intercellular CO$_2$ concentration ($C_i$), stomatal conductance ($G_s$) and transpiration rate ($T_r$), of each material were assayed using a programmable, open-flow gas exchange system (Li-6400, Li-Cor, USA) after 15 days of treatment.

A chlorophyll fluorescence imaging system (CF Imager, Technological Ltd. Colchester, UK) was used to determine the chlorophyll fluorescence parameters at the end of the 15-day treatment. After dark-adaptation in a dark chamber for 20 min, fresh samples (8 mm leaf disc) were positioned in the previously selected area of interest (AOI). Kinetics curves of the chlorophyll fluorescence parameters of the samples were displayed in the kinetics window of the software, while corresponding data like the maximal quantum yield of photosystem II (PSII) ($F_{v}/F_{m}$), the actual quantum yield of PSII ($\Phi_{PSII}$) and the nonphotochemical quenching (NPQ) were directly derived from the report window. Fluorescence spectra of plants were obtained every 4 days from the third day of treatment using a fluorescence spectrophotometer (F-4600, HITACHI, Japan) and an excitation wavelength of 436 nm, and the energy distribution photosystem I/ photosystem II (PSI/PSII) was calculated based on the methodology of Li et al. (2002).

Estimation of cell membrane injury

Lipid peroxidation of the cell membrane was estimated from cellular malondialdehyde (MDA) content using methodology modified from Xu et al. (2013). Leaf samples (0.1 g) were ground in 1.5 mL of extracting solution containing 10% trichloroacetic acid (TCA). After centrifugation, 1 mL of supernatant was mixed with 1 mL 0.6% thibabituric acid (TBA), and the resulting mixture was bathed in boiling water for 15 min, after which the cooled mixtures were analyzed spectrophotometrically at 450, 532, and 600 nm. MDA concentrations ($c_{MDA}$) were calculated using the equation $c_{MDA} = 6.45 \times (A_{532} - A_{600}) - 0.56 \times A_{450}$. 

Zhang et al. (2022), *Management of Biological Invasions* 13(2): 274–287, https://doi.org/10.3391/mbi.2022.13.2.02
**Determination of antioxidants**

Samples (0.1 g) were triturated in 1.5 mL of 95% methyl alcohol. After centrifugation, the supernatant of the samples was used to detect flavonoid and total phenol contents and total antioxidant capacity (TAC).

To measure the flavonoid content in the samples, 0.2 mL 5% NaNO₂, 0.3 mL 10% AlCl₃ and 1 mL 1 mol L⁻¹ NaOH were successively added to the 8-fold diluted supernatant above, and the mixture was analyzed spectrophotometrically at 510 nm, following the methodology of Ainsworth and Gillespie (2007). A standard curve was created to calculate flavonoid content using catechins.

We determined the total phenol content using the methodology described by Ainsworth and Gillespie (2007). The supernatants above were diluted with 95% methanol to 1 mL, after which 1 mL 10% foline-phenol and 2 mL 0.7 mol L⁻¹ Na₂CO₃ were added to the solution in turn. The solution was then analyzed spectrophotometrically at 765 nm. A standard curve was created to calculate the content of total phenols using gallic acid.

Using the method amended by Gangwar et al. (2014), the TAC of the samples was estimated by means of the radical scavenging reaction of 1,1-diphenyl-2-picrylhydrazyl (DPPH). Then, 0.15 mL of the resulting supernatant above was mixed with 3 mL 120 μmol L⁻¹ DPPH, and the mixture was analyzed spectrophotometrically at 517 nm. A standard curve was created to calculate the TAC of the samples via gradient dilution of the DPPH solution.

**Statistical analysis**

The data in this study are presented as means ± standard deviations (SD). Statistical analysis and comparison of differences between control and treatment groups were performed using SPSS 19.0 (IBM SPSS, Chicago, USA), with significance defined by a p-value of < 0.05. Graphs were produced using Origin Pro 8.0 (OriginLab, Northampton, MA, USA) and Adobe Photoshop CC 2014 (Adobe Systems Inc., USA).

**Results**

*Changes in photosynthetic pigment in S. calendulacea and S. trilobata under shading*

Photosynthetic pigment is the material basis for capturing light energy and, therefore, can be used as an indicator of the photosynthetic capability of plants. As shown in the Figure 2A and 2B, the contents of Chl a+b and Chl a of *S. calendulacea* under shading were significantly reduced (by 9.85% and 12.31%, respectively) compared to the control group, while no significant changes were observed in *S. trilobata*. The Chl b content significantly rose by 20.12% in *S. trilobata*, while the native species displayed no significant
Figure 2. The effect of shading on chlorophyll \( a+b \) content (A), chlorophyll \( a \) content (B), chlorophyll \( b \) content (C) and the ratio of chlorophyll \( a \) to chlorophyll \( b \) (D) of \( S. \) calendulacea and \( S. \) trilobata after the shading treatment. The data in this figure was presented as mean ± SD (\( n = 5 \)). Asterisks above columns indicate a statistical significance for comparisons between control group and shading group (Fm: fresh mass, ns: no significance, **\( p < 0.01 \) and ***\( p < 0.001 \)).

Changes after shading (Figure 2C). The ratio of Chl \( a \) to Chl \( b \) in \( S. \) trilobata declined significantly by 27.04%, but \( S. \) calendulacea showed no significant changes (Figure 2D).

Changes in photosynthetic gas exchange parameters in \( S. \) calendulacea and \( S. \) trilobata due to shading

After shading treatment, the \( P_n \) of both species investigated presented significant declines, with \( S. \) trilobata showing a smaller decrease (70.07%) than \( S. \) calendulacea (81.22%) (Figure 3A). The \( G_c \) and \( T_r \) of the two \textit{Sphagenticola} species also decreased, but in this case, the native species demonstrated a greater decrease (\( G_c: 86.04\%; T_r: 80.10\%) than the invasive species (\( G_c: 78.64\%; T_r: 77.15\%) (Figure 3B, C). The \( C_i \) of the materials showed no significant differences between control and shading groups (Figure 3D).

Changes in chlorophyll fluorescence parameters in \( S. \) calendulacea and \( S. \) trilobata due to shading

After shading, \( F_v/F_m \) dropped significantly, with a greater change in \( S. \) calendulacea (9.28%) than \( S. \) trilobata (4.02%) (Figure 4A). \( \Phi_{PSII} \), representing the activity of PSII, significantly decreased after treatment, and a sharper drop (by 23.17%) was observed for the native species (Figure 4B). A significant increase was detected in the NPQ of the materials, with...
Response of *S. trilobata* under shading

**Figure 3.** The change of photosynthetic parameters including $P_n$ (*A*), $G_s$ (*B*), $T_r$ (*C*) and $C_i$ (*D*) of *S. calendulacea* and *S. trilobata* under shading. The data in this figure was presented as mean ± SD ($n = 5$). Asterisks above columns indicate a statistical significance for comparisons between control group and shading group (ns: no significance, *p* < 0.05, **p** < 0.01 and ***p** < 0.001).

**Figure 4.** The chlorophyll fluorescence parameters including $F_v/F_m$ (*A*), $\Phi_{PSII}$ (*B*), NPQ (*C*) and fluorescence spectra (*D*) of *S. calendulacea* and *S. trilobata* during the shading treatment. CK-*S.c*, CK-*S.t*, S-*S.c* and S-*S.t* in (*D*) stand for *S. calendulacea* of control group, *S. trilobata* of control group, *S. calendulacea* of shading group and *S. trilobata* of shading group respectively. The data in this figure was presented as mean ± SD ($n = 5$). Asterisks above columns in (*A*), (*B*) and (*C*) indicate a statistical significance for comparisons between shading and control (**p** < 0.01 and ***p** < 0.001).

*S. calendulacea* exhibiting a greater increase (26.27%) than *S. trilobata* (22.87%) (Figure 4C).
During treatment, the PSI/PSII of the material from the shading group was always higher than that of the control group, but the trend was different between the two species. *S. trilobata* showed a downward trend from the third day and then leveled off on the eleventh day, while *S. calendulacea* decreased after ascending to a peak on the seventh day, leveled off on the eleventh day and became higher than the invasive species on the seventh day (Figure 4D).

**Oxidative damage and changes in antioxidant substances and capacity in *S. calendulacea* and *S. trilobata* due to shading**

Variations in content of MDA, a product of lipid peroxidation in the cell membrane, can indicate structural and functional cell membrane damage. After shading treatment, the MDA content in *S. calendulacea* significantly rose by 139.67%, but no significant change was observed in *S. trilobata* (Figure 5A).

Flavonoids and phenols are antioxidants that scavenge ROS from plants. Under shading, the flavonoid content of *S. calendulacea* decreased by 21.34% (Figure 5B). The total phenol content dropped significantly by 45.01% in *S. trilobata*, but no significant difference was observed in *S. calendulacea* after treatment (Figure 5C). The TAC of the invasive species demonstrated a significant and sharper decrease (78.61%), which was approximately 1.15 times that of the native species (67.95%, Figure 5D).
Discussion

Alien species not only colonize nutrient-rich habitats but, due to their high resource-use efficiency, can also survive in resource-poor environments (Funk and Vitousek 2007). Originating in middle South America, *S. trilobata* is now widespread in South China and has demonstrated the propensity to establish monodominant populations in wastelands due, in large part, to its high tolerance to high temperatures (Cai et al. 2021) and high irradiance (Song et al. 2009a). Nevertheless, *S. trilobata* has been discovered at the edge of the forest (Cao et al. 2007; Song et al. 2009b), indicating that this invader is adaptable to low-light environments. Recent examinations of the effects of different light levels on multi-invasive plants and noninvasive plants in South China (Hou et al. 2014) and invasive *Impatiens glandulifera* under shading (Gruntman et al. 2019) indicate that invasive alien plants are more capable of using light under different levels of irradiance than noninvasive plants. Here, *S. trilobata* and *S. calendulacea* have been used to investigate differences in oxidative damage and physiological and ecological responses of photosynthesis in low-light versus normal-light habitats in order to better understand this species’ biological invasion mechanism(s).

Stronger photosynthetic capacity of *S. trilobata* under low-light conditions

Decreases in irradiance cause physiological changes in plants, including changes in photosynthetic capacity. Studies have shown that higher levels of Chl \(a+b\) and Chl \(b\) and lower Chl \(a/b\) levels improve the ability of plants to absorb scattered light and survive under low-irradiance conditions (Valladares and Niinemets 2008; Kume et al. 2018). Here, the invader, *S. trilobata*, exhibited a stronger light-harvesting ability than the indigen. Although Chl \(a+b\) levels of the two *Sphagmecola* species both decreased after shading, the Chl \(b\) content of *S. trilobata* rose, leading to a significant drop in Chl \(a/b\) (Figure 2), suggesting *S. trilobata* might have a greater light-harvesting ability in low-light environments, making them using light resources more efficiently. Similarly, research on physiological changes in the invasive aliens *Ageratina adenophora* and *Chromolaena odorata* and in the noninvasive alien *Gynura* sp. under different levels of light suggest that invasive species possess superior resource-capture-related traits and light adaptability than noninvasive species (Feng et al. 2007). Variations in gas exchange parameters can infer differences in photosynthetic capacity, and previously published literature has shown that reductions in gas exchange parameters in shade-tolerant genotypes are smaller than those observed in shade-sensitive genotypes in the same species (Sundari 2009). In the present study, we observed lower reductions in \(P_o\), \(G_s\), and \(T_r\) in *S. trilobata* (Figure 3), indicating its greater photosynthetic capacity and protection against shading compared to *S. calendulacea*. The advantage in light-harvesting and photosynthetic capacity enables the invader to defeat the
indigen in the competition for light energy, thus expanding its invasion in low light environment.

Chlorophyll fluorescence is closely related to photosynthesis and can reflect physiological changes in photosynthesis. \( F_v/F_m \) values decrease under stress (Murchie and Lawson 2013); and, because Chl \( a+b \) declines under severe shading, the activity of PSII will also decrease, thereby further reducing \( \Phi_{\text{PSII}} \) (Miralles et al. 2011). Under stress, excess light energy, which is not involved in photochemical reactions due to decreasing \( \Phi_{\text{PSII}} \), will transform into heat dissipation or chlorophyll fluorescence to prevent internal cell damage, after which NPQ levels will increase (Maxwell and Johnson 2000; Fu et al. 2012). Both \( F_v/F_m \) and \( \Phi_{\text{PSII}} \) decreased, while NPQ increased in the two \textit{Sphagmaticola} species investigated in the present study, but the invasive species demonstrated slighter change (Figure 4A, B, C). This result indicates that \textit{S. trilobata} was not only less affected by shading, but also had a higher light utilization efficiency rather than \textit{S. calendulacea}, further revealing a tendency to invade low light environment. Moreover, PSI/PSII values enhancement in \textit{S. calendulacea} were larger than those in \textit{S. trilobata} (Figure 4D), a lower PSI/PSII ratio indicates higher photosynthetic capacity (Li et al. 2002).

\textit{Lower oxidative damage in \textit{S. trilobata} under low light}

Shading can give rise to oxidative damage in plant cells, leading to increased MDA content (Zhang et al. 2018). In our experiments, shading elevated MDA content in \textit{S. calendulacea}, while \textit{S. trilobata} remained unchanged (Figure 5A). These results demonstrate that oxidative damage occurs in the native species in low-light environments but not in the invasive species, supporting the increased survival rates observed in shade for invader versus native species.

Flavonoids and phenols are nonenzymatic antioxidants that can scavenge ROS (Fini et al. 2011; Agati and Tattini 2010), and their contents and TAC are both effective indicators for assessing oxidative damage in plants (Boo et al. 2011). Compared with \textit{S. calendulacea}, \textit{S. trilobata} displayed greater decreases in total phenol content and TAC (Figure 5C, D). This phenomenon and the slight change in MDA both indicate less oxidative damage in \textit{S. trilobata}, which enables the invader to devote more resources to photosynthesis, explaining its greater photosynthetic capacity and protection against shading and enhancing its growth in low-irradiance environments compared to the indigene. Similar finding was also reported in invasive weed \textit{Mikania micrantha} (Jiang et al. 2021), the synthesis of photoprotective substance like flavonoid was decreased and more resources were allocated into the growth of stem under shading environment. Therefore, we hypothesize that \textit{S. trilobata} is better able to utilize light under different levels of irradiance than \textit{S. calendulacea}, which may be the key to its invasion in low-light environments.
In conclusion, S. trilobata appears to possess a survival advantage in low-light environments. Compared to S. calendulacea, S. trilobata exhibited less inhibition of photosynthesis and less oxidative damage due to shading treatment. Although these results provide a theoretical basis for predicting potential invasion areas of S. trilobata and the prevention in low-light environments such as forest margins, further study is needed to understand molecular mechanism in photosynthesis under different light conditions.

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Authors’ contribution

Jun-jie Zhang: data curation, formal analysis, investigation, writing – original draft; Min-ling Cai: investigation, methodology, writing – original draft; Li-hua Chen: writing – review and editing, validation; Xiao-hua Lin and Jin-di Peng: investigation; Jun-dong Huang: software; Ling Shao: writing – review and editing; Chang-lian Peng: funding acquisition, project administration, resources, supervision, writing – review and editing.

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