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ORIGINAL ARTICLE

Photosynthetic compensation of non-leaf organ stems of the invasive species *Sphagneticola trilobata* (L.) Pruski at low temperature

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Abstract

Biological invasion is a hot topic in ecological research. Most studies on the physiological mechanisms of plants focus on leaves, but few studies focus on stems. To study the tolerance of invasive plant (*Sphagneticola trilobata* L.) to low temperature, relevant physiological indicators (including anthocyanin and chlorophyll) in different organs (leaves and stems) were analyzed, using a native species (*Sphagneticola calendulacea* L.) as the control. The results showed that, upon exposure to low temperature for 15 days, the stems of two *Sphagneticola* species were markedly reddened, their anthocyanin content increased, chlorophyll and chlorophyll fluorescence parameters decreased, and the accumulation of reactive oxygen species in the stem increased. The percentage increases of antioxidants and total antioxidant capacities in stems were significantly higher in *S. trilobata* than in *S. calendulacea.* This showed that *S. trilobata* had higher cold tolerance in stems while leaves were opposite. To further verify the higher cold tolerance of the stem of *S. trilobata,* a defoliation experiment was designed. We found that the defoliated stem of *S. trilobata* reduced anthocyanin accumulation and increased chlorophyll content, while alleviating membrane lipid damage and electrical conductivity, and the defoliated stem still showed an increase in stem diameter and biomass under low temperature. The discovery of the physiological and adaptive mechanisms of the stem of *S. trilobata* to low temperature will provide a theoretical basis for explaining how *S. trilobata* maintains its annual growth in South China. This is of great significance for predicting the future spread of cloned and propagated invasive plants.

Keywords *Sphagneticola trilobata* (L.) pruski · Stem · Photosynthesis · Anthocyanin

Abbreviations

Chl *a* (*b*)	Chlorophyll *a* (*b*)
Chl	Total chlorophyll
DAB	Diaminobenzidine
DPPH	1,1-Diphenyl-2-picrylhydrazyl
ETR	Electron transport rate
F_0	Minimum fluorescence
F_m	Maximum fluorescence yield of the dark-adapted state
F_m'	Maximum fluorescence yield of the light-adapted state
F_s	Steady-state fluorescence
F_v/F_m	Maximal quantum yield of PSII photochemistry
MDA	Malondialdehyde
NBT	Nitroblue tetrazolium
ROS	Reactive oxygen species
TBA	Thiobarbituric acid
TCA	Trichloroacetic acid
Φ_{PSII}	Actual quantum yield of PSII

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Introduction

Biological invasion refers to an organism entering a new area from its original distribution area. These invasive species reproduce, spread rapidly, and survive for a long time in their new environments (Hoffmann and Courchamp 2016). Plants are among the most widely distributed invasive

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species. Research shows that many exotic organisms have successfully invaded China (Huang et al. 2009; Wang et al. 2003). These invasive species not only threaten the diversity of organisms and change the structure and function of ecosystems but also bring huge economic losses to the invaded areas (Early et al. 2016).

Previous studies have shown that phenotypic plasticity, genetic differentiation, lack of natural enemies, and allelopathy are important mechanisms for successful invasion by invasive species (Gioria and Osborne 2014). Among them, phenotypic plasticity is the main method to address the variation in environmental factors (Fusco and Minelli 2010). When limited resources are available for plant organs, trade-offs occur. In unusual environmental conditions, these trade-offs cause species to distribute widely and cause plants to have different characteristics in different environments (Tuller et al. 2018). However, a close relationship has been found between interorgan resource trade-offs and phenotypic plasticity. At present, there are two different adaptive responses in plants under different environmental conditions: (1) simultaneous traits optimization and (2) dynamic traits changes to adapt to prevailing conditions. This phenomenon is called phenotypic plasticity (Xiao and Dean 2016). Phenotypic plasticity has been thought to promote biological invasion. It ensures that a species can maintain appropriate ecological and physiological performance in a novel environment. Species that exhibit phenotypic plasticity have better adaptability to different light levels, temperature conditions, and soil nutrient conditions in the invasion areas. For example, *Mikania micrantha* produces a large number of light seeds and had a rapid reproductive capacity (Shen et al. 2016), and *Ipomoea cairica* adapts well to changing water availability by changing its allelopathy and biomass allocation patterns (Takao et al. 2011). Studies have demonstrated that the phenotypic plasticity of plants is often closely related to the trade-offs in the allocation of resources among organs (Murren et al. 2015). When limited resources are allocated to different morphological characteristics, the increase in one characteristic leads to the decrease in another, and this trade-off in the allocation of resources is an important driver of plant phenotypic plasticity (Gratani 2014). The trade-off phenomenon is widespread and takes different forms in different environments. For example, changes in aboveground biomass (Loeser et al. 2004), resource allocation (Wang et al. 2016), and reproductive strategy generally appeared after defoliation (Ida et al. 2012). In a previous study, *M. micrantha* redistributed nutrients and preferentially distributed newly synthesized substances from the roots to the aboveground parts, which compensated for the loss of leaf photosynthetic organs (Li et al. 2013). *Ambrosia artemisiifolia* and *Pennisetum centrasiaticum* preferentially transfer underground resources to aboveground parts, increasing aboveground biomass by reducing the root–shoot ratio (Gard et al. 2013). Therefore, biologists believe that invasive plants are usually exposed to various environmental conditions and that their successful invasion is associated with rapid ecological differentiation, which might be due to their having greater phenotypic plasticity than native species (Davidson et al. 2011). Because plasticity of physiological and morphological characteristics provides more ways to cope with limited resources, invasive species might benefit from plasticity in low-resource or variable environments. Phenotypic plasticity is a major mechanism by which plant becomes invasive species.

Sphagneticola trilobata (L.) Pruski (Asteraceae), a widespread invasive species in South China, is native to tropical America. Compared with the local species *Sphagneticola calendulacea* (L.) Pruski, the leaves of *S. trilobata* can better adapt to low-light environment by improving their CO_2 fixation ability and quantum efficiency of light utilization (Song et al. 2010; Sun et al. 2015). In a water-limited environment, *S. trilobata* can reduce the cost of leaf construction (Song et al. 2009). In addition, the leaves of *S. trilobata* can affect the soil microbial community structure by producing allelochemicals, thus inhibiting the growth of surrounding plants and leading to a successful invasion (Coats and Rumpho 2014). Under high-temperature, high-light condition in summer, the leaves of *S. trilobata* turn obviously red and adapt to the oxidative environment by accumulating a large content of anthocyanins (Feild et al. 2001; Zhang et al. 2012a). As leaf is the most important organ for photosynthesis, it is a sensitive organ during plant evolution. Hitherto, research on the invasion mechanism of *S. trilobata* has mainly focused on the phenotypic plasticity of leaves in adverse conditions. However, defoliation is a common phenomenon throughout life history of plants. In some adverse condition, plant leaves will wilt and wither. Some non-leaf organs, such as stems, play an important role in maintaining normal plant development (Yang et al 2006). At present, few studies have reported on the phenotypic plasticity of non-photosynthetic organ stems of invasive plants in different environments, and most of these studies have focused on crops (Wang et al. 2001).

Sphagneticola trilobata prefers hot and humid environments. Its pollen vigor and stigma receptivity are poor. There have been no reports on its seed germination. *S. trilobata* mainly reproduces asexually, and its stem segment is highly plastic. It can expand rapidly through cutting, stripping, and soilless cultivation, and rapidly expands its invasion area throughout the year. In terms of life history, *S. trilobata* and *S. calendulacea* are distributed in a mosaic pattern along riverbanks and coastal wet zones in South China. Investigations have shown that compared with *S. trilobata*, *S. calendulacea* has higher cold tolerance, and its distribution area could extend from the southern subtropical zone to the temperate zone (Sun et al. 2015). South China is affected by the

subtropical monsoon climate and has distinct dry and wet seasons. Summer is hot and humid, while winter is cold and cloudy. From the latter half of winter to the onset of the rainy season, low temperature is common. Many subtropical plants are thus impacted by low-temperature conditions. Sun et al. (2015) showed that the tolerance of the leaves of *S. trilobata* is not as high as that of native species under extremely low temperatures, and the leaves of the invasive plant show chlorosis and wilting.

However, *S. trilobata* grows rapidly throughout the year in South China. Some studies have found that *S. trilobata* has the potential to continue to spread to inland regions of China. At present, it is also distributed in Jiangsu, Chongqing, and other regions (Liu et al. 2013). It is unclear how this spread is related to the phenotypic plasticity of the stem at low temperature, and whether using this strategy to cope with a low-temperature environment helps *S. trilobata* spread to temperate regions, thus threatening the survival of the existing distribution of *S. calendulacea*. Therefore, the physiological and ecological characteristics and adaptive mechanisms of the stem of *S. trilobata* were studied under a low temperature. This study is profoundly significant for predicting the future trends in the clonal propagation of invasive plants and adopting effective management methods.

Material and methods

Material culture and treatment

Sphagneticola trilobata and *S. calendulacea* are widely distributed in the riparian, coastal, and other humid environments of the subtropics in China. In this study, plant material was collected from the campus of South China Normal University, Guangzhou, China (23° 08′ 47.90″ N, 113° 21′ 15.32″ E). *S. trilobata* and *S. calendulacea* were identified according to previous reports performed by our laboratories or other researchers (Sun et al. 2015; Wu et al. 2013). In addition, the materials involved in this study were deposited at the Herbarium of the South China Botanical Garden (IBSC) with the deposition number 806,219 for *S. trilobata* (L). Pruski and 806,217 for *S. calendulacea* (L). Pruski. Cut shoots with buds were propagated in an incubator (light intensity 100–120 μmol m^{-2} s^{-1}, culture temperature 28/25 °C, day/night). After rooting, the regenerated seedlings with approximately the same size and height were selected and transplanted into pots, with 3 plants per pot. When the length of the stem reached 20–30 cm, the plants were used for the experiments.

To compare the tolerance of different organs (leaves and stems) of the plant species to low temperature, the two species cultured at room temperature were moved to a low-temperature culture room (15 ± 1 °C) (the average temperature in winter in South China is approximately 15 °C) for 15 days. Leaves and stems at the third to fifteenth leaf positions were selected as experimental materials on the days 0 and 15 of treatment. To further verify the compensatory effect of plant stems at low temperature, a defoliated experiment was designed. Plants cultured at room temperature were transplanted to a low-temperature culture room (15 ± 1 °C) for 15 days. Among them, 1/2 of the subjects were randomly chosen for defoliation treatment, while the remaining 1/2 of the plants were not defoliated as control. Stems at the third to fifth leaf positions were chosen as experimental materials on days 0 and 15 of treatment, respectively.

Determination of chlorophyll fluorescence parameters

The chlorophyll fluorescence parameters of *S. trilobata* and *S. calendulacea* were measured using a chlorophyll fluorescence imaging system (CF Imager, Technological Ltd. Colchester, UK) at low temperatures. Five 8-mm leaf discs and five 1-cm stem segments were placed in 12-well plates (each hole was filled with water), respectively. The leaf discs and stem segments were dark-adapted for 20 min prior to fluorescence determination. The minimum fluorescence (F_o) was determined with measuring light less than 0.05 μmol m^{-2} s^{-1}. The maximum fluorescence (F_m) was induced by a 1-s pulse of saturating light [6162 μmol m^{-2} s^{-1}]. The maximal quantum yield of PSII photochemistry (F_v/F_m) was calculated as $(F_m - F_o)/F_m$ (Oxborough and Baker 1997). Subsequently, the steady-state fluorescence (F_s) and maximum fluorescence (F_m') were recorded under 400 μmol m^{-2} s^{-1} actinic light. The actual quantum yield of PSII (Φ_{PSII}) and the electron transport rate (ETR) were calculated according to Genty et al. (1989). The formulas were as follows: $\Phi_{PSII} = (F_m' - F_s)/F_m'$, $ETR = \Phi_{PSII} \times PPFD \times 0.5 \times 0.85$.

Anthocyanin content determination

Leaves (0.05 g) and stems (0.05 g) were soaked in 2 mL 1% HCl-methanol (v/v) for 6 h in darkness. To remove chlorophyll, 1 mL chloroform and 0.5 mL pure water were added to a 1-mL extract. After being fully mixed, the solution separated into two layers: chlorophyll was dissolved in the lower chloroform phase, and anthocyanin was dissolved in the upper methanol–water phase. The volume of the upper solution was measured, and the absorption value at 530 nm was determined using a UV–Vis 2450 spectrophotometer (Shimadzu, Tokyo, Japan). The anthocyanin content in the leaves and stems was calculated using cyanidin-3-O-glucose as a standard curve (5–200 μM).

Determination of chlorophyll content

Leaves (0.05 g) and stems (0.05 g) were placed in 10 mL centrifuge tubes. They were quickly crushed with metal rods, and liquid nitrogen was added. Then 4 mL 80% acetone solution was added; the tube was shaken well, the cap was tightened, and the solution was extracted overnight at 4 °C. The absorbance of the extract was determined at 663 nm and 645 nm using a UV–Vis 2450 spectrophotometer, and 80% acetone was used as a blank control. The contents of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), and total chlorophyll (Chl) were calculated according to Wellburn (1994).

Localization of reactive oxygen species in tissue

Chemical localization and detection of hydrogen peroxide

After a low-temperature treatment for 15 days, leaf and stem segments (approximately 2–3 cm) were immersed in a dish containing 0.5 mg mL^{-1} diaminobenzidine (DAB) (using pH 7.0 phosphate buffer as solvent), covered with gauze for 15 min, and then placed in darkness for more than 8 h. The accumulation of ROS could be observed as brown spots after DAB staining. Subsequently, the stained leaves and stems were boiled in 95% ethanol to remove chlorophyll (Liu et al. 2014). Finally, pictures were taken with a camera.

Chemical localization and detection of superoxide anions

After 15 days of low-temperature treatment, leaves and stems (approximately 2–3 cm) were immersed in glass dishes containing 0.1% nitroblue tetrazolium (NBT) and 10 mmol L^{-1} sodium azide (using pH 6.4 phosphate buffer as solvent). The gauze was vacuum-covered for 15 min and then placed in darkness for more than 2 h. The samples were monitored for the appearance of indigo blue spots. The chlorophyll was removed by bleaching the sample in a boiled ethanol solution (95%, v/v) (Sim et al. 2006). Finally, pictures were taken with a camera.

Determination of antioxidants

The leaves and stems were weighed at 0.05 g, ground with 2 mL 95% methanol (v/v), and centrifuged at 13,000 rpm at 4 °C for 10 min. The supernatant was used to determine the antioxidant indexes such as those of flavonoids and total phenols.

Determination of flavonoid content

The sample solution was diluted 8 times by the addition of 2 mL to 200 mL 5% $NaNO_2$, 300 mL 10% $AlCl_3$, and 1 mL of 1 mol L^{-1} NaOH in turn. After mixing completely, the absorbance value was determined at 510 nm. The standard curve of catechins (25–1000 mol L^{-1}) was established to calculate the total flavonoids in the samples.

Determination of total phenol content

The supernatant (800 µL) was diluted with 1 mL of 95% methanol, 1 mL 10% Folin phenol reagent, and 2 mL of 0.7 mol L^{-1} Na_2CO_3. Upon mixing, the solution changed color at room temperature. The absorbance at 765 nm was determined. The standard curve was established with gallic acid (25–250 mol L^{-1}), and the content of absolute phenol was calculated.

Determination of DPPH scavenging capacity

DPPH (1,1-diphenyl-2-picrylhydrazyl) solution (120 µmol L^{-1}) was prepared with 95% methanol. The absorbance at 517 nm was determined by adding 3 mL DPPH solution to 150 µL sample solution, with 95% methanol as a blank control. The standard curve was established by gradient dilution of the DPPH solution (10–120 µmol L^{-1}), and the DPPH scavenging capacity of the sample was calculated.

Determination of stem diameter and biomass

Determination of stem diameter

During the low-temperature treatment, vernier calipers were used to measure the diameter of plant stem segments (with the second internode as the criterion). Five replicates were used to record the length of the stem diameter at 0 day and 15 days, respectively.

Determination of stem biomass

The stems of plants were harvested after days 0 and 15 of low-temperature treatment and then packed into different envelopes. The stem was dried to a constant weight in an oven at 75 °C, and the dry weight was measured. The experiment was replicated five times.

Determination of membrane destruction in cells

Malondialdehyde (MDA)

Stem segments of 0.1 g were weighed, and 2 mL 10% trichloroacetic acid (TCA) was added to grind the homogenate. Then they were transferred to 2 mL centrifuge tubes and centrifuged for 10 min at 4000 rpm. 1 mL supernatant was moved to a new centrifugal tube and placed on ice for testing. 1 mL 0.6% thiobarbituric acid (TBA) was added to each centrifuge tube, mixed well, and boiled in a boiling water bath for 30 min.

It was then cooled quickly on ice. The absorbance values of the supernatant after reaction were determined at 532, 600, and 450 nm wavelengths. The MDA contents were calculated using the formula: C_{MDA} (mol L^{-1}) = 6.45 × (OD_{532} − OD_{600}) − 0.56 × OD_{450}.

Electrolyte permeability

Two stem segments (1 cm) were placed in a centrifuge tube filled with 3 mL superfluous water and then placed in a test tube filled with 10 mL double-steamed water. After standing at room temperature for 3 h, the electrical conductivity of the exudate in R_1 was measured by a conductivity meter (PP-15-P11, Sartorius, Germany). Then, the test tube was kept in a boiling water bath for 45 min to kill living tissues. After cooling to room temperature, the conductivity in R_2 was measured by the abovementioned method expressed as the relative conductivity (%). The leakage rate of the plasma membrane was calculated as R_1/R_2. The experiment was replicated five times.

Statistical analysis

The data represent the means ± standard error (SE) of five samples in the experiment. The statistical analysis and multiple data comparisons were performed using IBM SPSS Statistics 19.0 (IBM, NY, USA). Duncan multiple comparison method was used to test the significance of the differences among groups, and differences were considered significant at $p < 0.05$. Figures were constructed using SigmaPlot 12.5 (Systat Software, San Jose, CA, USA).

Results

Comparisons of the tolerance of leaves and stems of two *Sphagneticola* species under low temperature

Changes in the phenotype of two Sphagneticola species

After 15 days of low-temperature treatment, the leaves of both *Sphagneticola* species showed partial but not obvious reddening that was mainly concentrated at the base of the leaves. The leaves of *S. trilobata* also showed a yellowing phenomenon. Interestingly, though the stems of both *Sphagneticola* species showed significant reddening, the *S. trilobata* stems after 15 days of low-temperature treatment were much redder than the native species (Fig. 1).

Changes in the non-photosynthetic pigments and photosynthetic pigments in two *Sphagneticola* species

Anthocyanin is a non-photosynthetic pigment. Under the low-temperature treatment, the leaves and stems of both

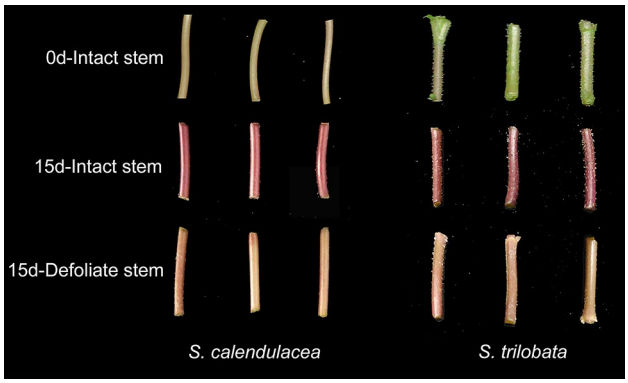

Fig. 1 The stem phenotype of *Sphagneticola* after different treatments. The picture shows the phenotypic changes in the stems of two *Sphagneticola* species (0-day intact stem, 15-day intact stem) after a low-temperature treatment for 0 and 15 days. To further study the compensatory effect in the stem, the phenotypic changes in intact and defoliated stems of *Sphagneticola* were compared after 15 days of low temperatures (15-intact stem and 15-defoliated stem) ($n = 5$)

Sphagneticola species turned red due to the accumulation of anthocyanins. In the leaves, the anthocyanin accumulation increased by 205% and 251% in the native and invasive species, respectively, which were similar increases (Fig. 2a). However, in the stems, anthocyanin accumulation was nearly 8 times higher in *S. trilobata* (310%) than in *S. calendulacea* (43%) (Fig. 2b). These results are consistent with the stem reddening in *S. trilobata* being significantly higher than in *S. calendulacea* (Fig. 1).

Chlorophyll is an important photosynthetic pigment. In the leaves of *S. calendulacea*, Chl *a*, Chl *b* and Chl all increased under 15 days of low temperature. In contrast, the content of the photosynthetic pigments in the leaves of *S. trilobata* decreased under treatment (Fig. 2c, e, g). In addition, the photosynthetic pigments in the stems were decreased in the two *Sphagneticola* species. Among them, the decreases in Chl *a* and Chl *b* content in *S. trilobata* were slightly smaller than those in *S. calendulacea* (Fig. 2d, f), and the decrease in total chlorophyll pigment content was also smaller (39%), at nearly 3/4 of that in the native plants (52%) (Fig. 2h).

Changes in the chlorophyll fluorescence parameters of the two *Sphagneticola* species

At low temperature, the F_v/F_m of the leaves of both *Sphagneticola* species decreased with the prolongation of the low-temperature treatment. The decrease was 11.60% in *S. trilobata*, which was 3 times that in *S. calendulacea* (4.06%) (Fig. 3a). The F_v/F_m of the stems of the two plants also had the same downward trend as the leaves. However, the decline rate of *S. calendulacea* was 8.18%, nearly twice that of *S. trilobata* (4.32%) (Fig. 3b). The Φ_{PSII} and ETR can reflect

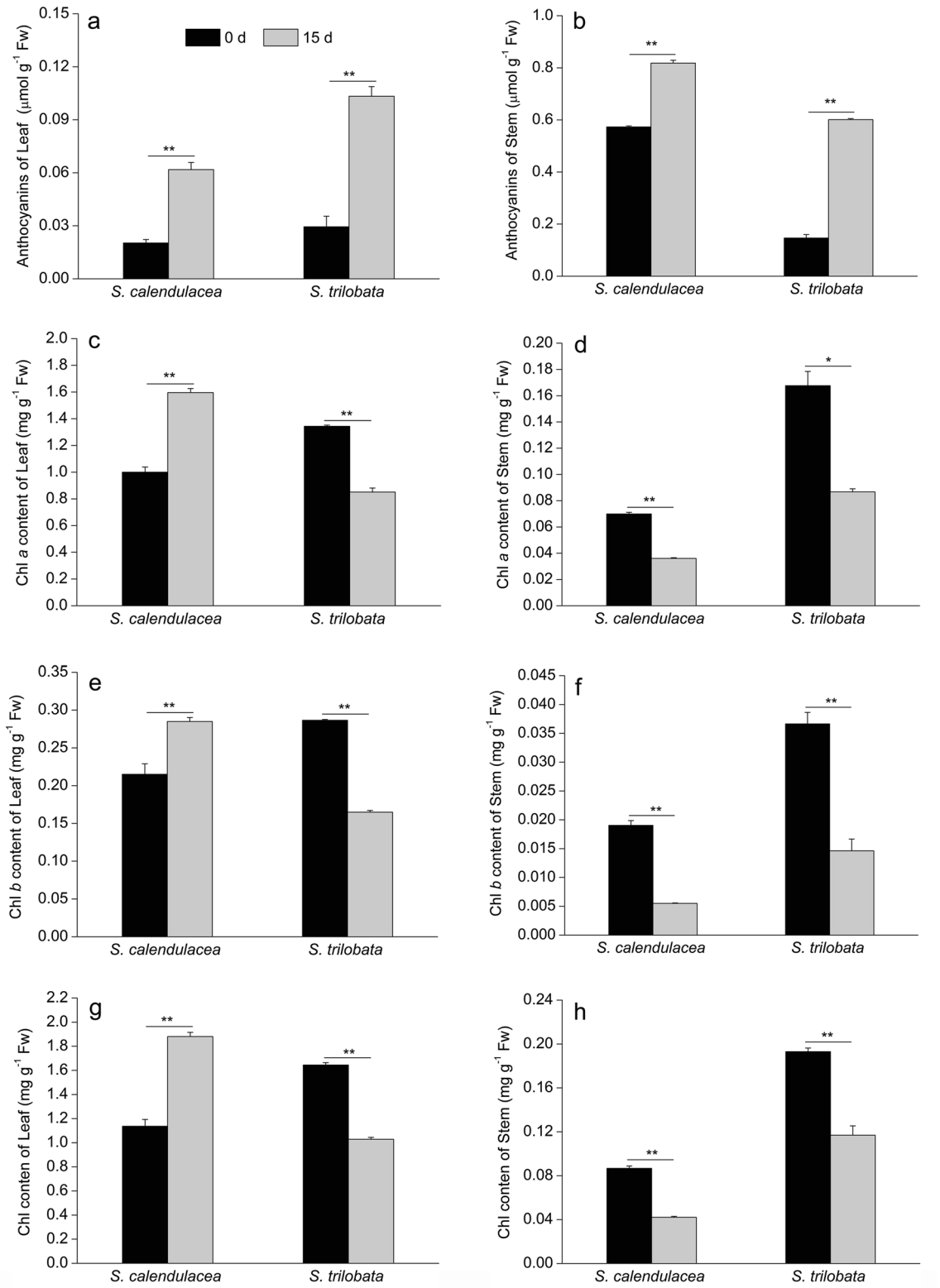

Fig. 2 Changes in anthocyanin and photosynthetic pigments in the leaves and stems of two *Sphagneticola* species at low temperature. Panels **a** and **b** represent the changes in the anthocyanin contents of leaves and stems, Panels **c** and **d** represent the changes in the Chl *a* contents in leaves and stems, Panels **e** and **f** represent the changes in the Chl *b* contents, and Panels **g** and **h** represent the changes in total Chl content in leaves and stems ($n=5$). * indicates a significant difference between 0 and 15 days after low-temperature treatment ($0.01<p<0.05$); **indicates an extremely significant difference between 0 and 15 days after low-temperature treatment ($p<0.01$)

the activity of PSII, and related to the photosynthetic rate of plants. The results showed that the leaves and stems in Φ_{PSII} and ETR of the two plant species showed downward trends under the low-temperature treatment. The leaf in Φ_{PSII} of *S. calendulacea* (1.96%) was less than that of *S. trilobata* (3.58%) while the stem in Φ_{PSII} of *S. calendulacea* (10.32%) was larger than that of *S. trilobata* (6.41%) (Fig. 3c, d). Similarly, the changes in the *ETR* of the leaves and stems of the two plant species at low temperatures had the same trend as that in Φ_{PSII} (Fig. 3e, f).

Localization of reactive oxygen species in the two *Sphagneticola* species

Generally, low temperatures lead to excess light energy not being utilized by photosynthesis, and a large amount of

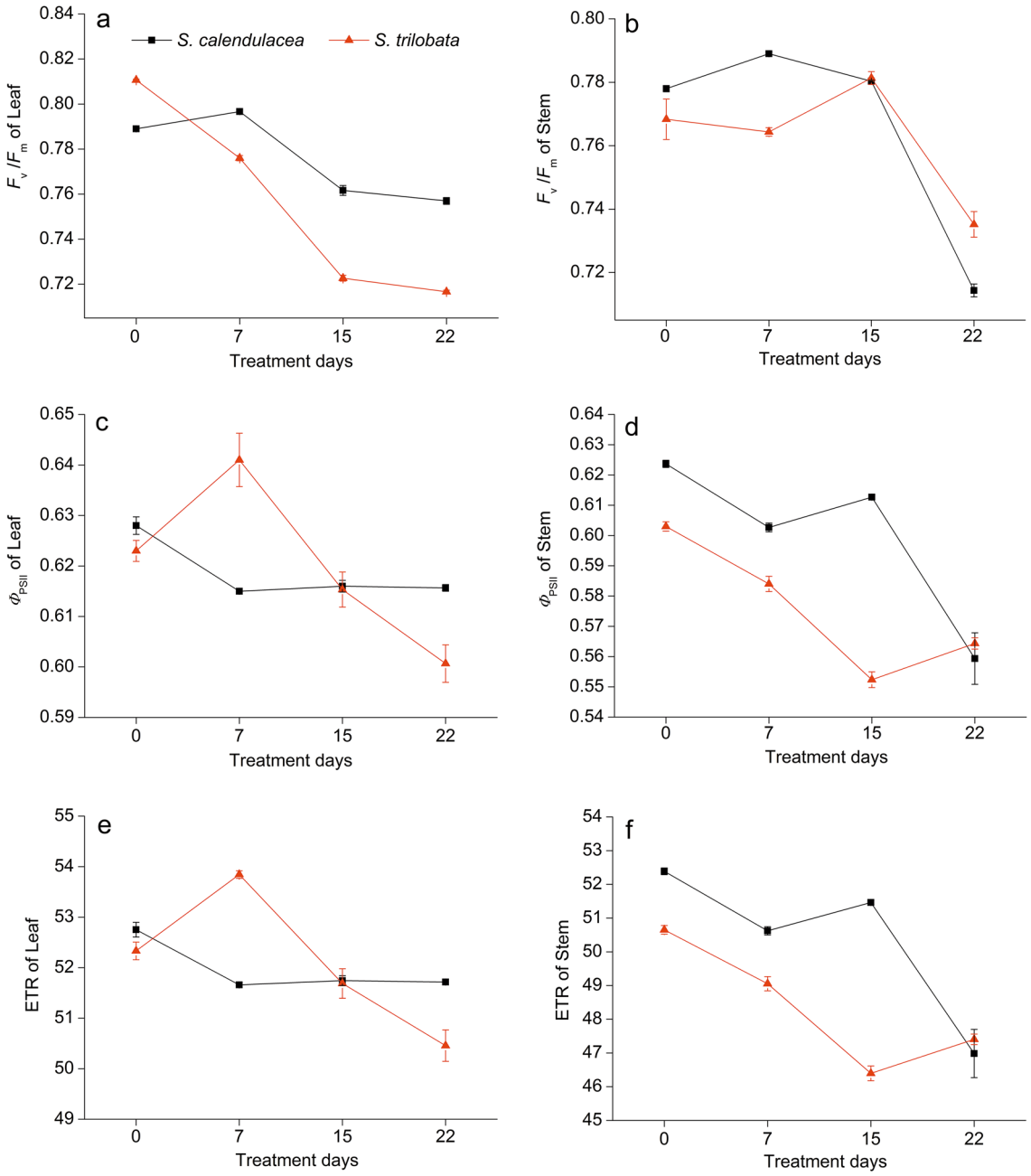

Fig. 3 Chlorophyll fluorescence parameters of leaves and stems from two *Sphagneticola* species at low temperature with time. Panels **a** and **b** represent the trends of maximal quantum yield of PSII photochemistry (F_v/F_m) of leaves and stems of the two *Sphagneticola* species; Panels **c** and **d** represent the trends in the actual quantum yield of PSII (Φ_{PSII}) of leaves and stems; and Panels **e** and **f** represent the trends in the electron transfer rate (ETR) of leaves and stems, respectively ($n=5$)

reactive oxygen species accumulates in the tissues (Soengas et al. 2018). In this study, the localization of reactive oxygen species (ROS) in the tissue showed that both leaves and stems had accumulated ROS under low temperature, including superoxide anion (Fig. 4a) and hydrogen peroxide (Fig. 4b), The accumulation of ROS in the leaves of *S. trilobata* was higher than that in native plants. In contrast, the accumulation of ROS in the stem of *S. trilobata,* which mainly occurred at the top and bottom ends of the stem segments, was less than that in *S. calendulacea* stem.

Changes in antioxidant contents in the two *Sphagneticola* species

Normally, the active oxygen scavenging system in plants maintains a balanced presence of ROS. However, changes in the external environment (e.g., low temperature) can lead to the accumulation of ROS in plants. Some studies have shown that ROS could be removed by increasing antioxidant activity (Xu et al. 2017). Consistent with this, the present study found that the antioxidant substances increased in the leaves and stems of *S. trilobata* and *S. calendulacea* under low-temperature treatment. The antioxidant substances, including flavonoids and total phenols in the leaves of *S. trilobata*, increased less than those in the native plants (Fig. 5a, c). In contrast, the antioxidant substances in the stems increased more in *S. trilobata* (Fig. 5b, d). The increase in total antioxidant capacity of the leaves of *S. trilobata* (245%) was less than that of the native leaves (298%) (Fig. 5e), but the increase in the total antioxidant capacity (546%) of the *S. trilobata* stems was nearly twice as much as that of the native species stems (258%) (Fig. 5f).

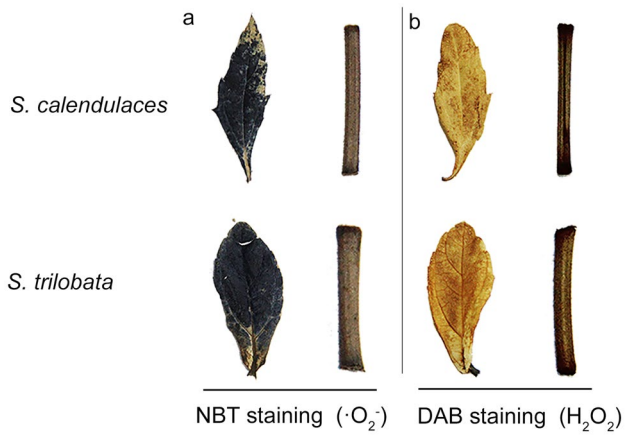

Fig. 4 The accumulation of reactive oxygen species (ROS) in the leaves and stems of two *Sphagneticola* species under low temperatures. Panel **a** shows the changes in superoxide anion ($\cdot O_2^-$) in the leaves and stems of the two *Sphagneticola* species after NBT staining. Panel **b** shows the changes in hydrogen peroxide (H_2O_2) in the leaves and stems of the two *Sphagneticola* species after DAB staining

Photosynthetic compensation in the stems of the two *Sphagneticola* species under low temperature

Phenotypic changes in the intact and defoliated stems

To further study the photosynthetic compensatory effect of the stem of *S. trilobata* under low temperature, a defoliation experiment was conducted. Compared to the 0-day treatment, the stems of the two *Sphagneticola* species had turned red after 15 days of low-temperature treatment. The defoliated stems of *S. trilobata* and *S. calendulacea* showed a decrease in redness compared to the intact stem. The phenotypic changes were the most noticeable in *S. trilobata* (Fig. 1).

Changes in photosynthetic pigments and non-photosynthetic pigments in the intact and defoliated stems

Pigments in plant tissues are mainly classified into two categories: photosynthetic pigments, such as chlorophyll, and non-photosynthetic pigments, which are mainly anthocyanins. Compared to that at 0-day treatment, the anthocyanin content of the intact and defoliated stems increased in both *Sphagneticola* species. *S. trilobata* had the smallest increase in anthocyanin in the defoliated stem (317%) (Fig. 6a). There were different trends in chlorophyll content in the two species. Compared to that at 0-day treatment, Chl *a* content decreased in the stems of the two *Sphagneticola* species under low temperature and the lowest decrease in content was observed in the defoliated stem of *S. trilobata* (13%) (Fig. 6b). Interestingly, in contrast to the intact stems, the contents of Chl *b* and Chl in the defoliated stem of *S. trilobata* were increased by 35% and 16%, respectively. The Chl *b* contents of *S. calendulacea* were also increased in the defoliated stems, while total Chl were decreased under low temperature (Fig. 6c, d).

Changes in the degree of cell membrane lipid damage in the intact and defoliated stems

Malondialdehyde (MDA), the final product of membrane lipid peroxidation, and cell membrane permeability are reliable indicators of cell membrane damage (Ellouzi et al. 2011). When MDA content and cell membrane permeability increase, the cell membrane damage is serious, probably due to excessive free radical accumulation. Compared to 0-day treatment, the MDA content in the intact and defoliated stems of the two *Sphagneticola* species increased, while the percent increase in MDA content in the defoliated stem of *S. trilobata* was smallest after 15-day low-temperature treatment (Fig. 7a). Similarly, relative membrane leakage showed

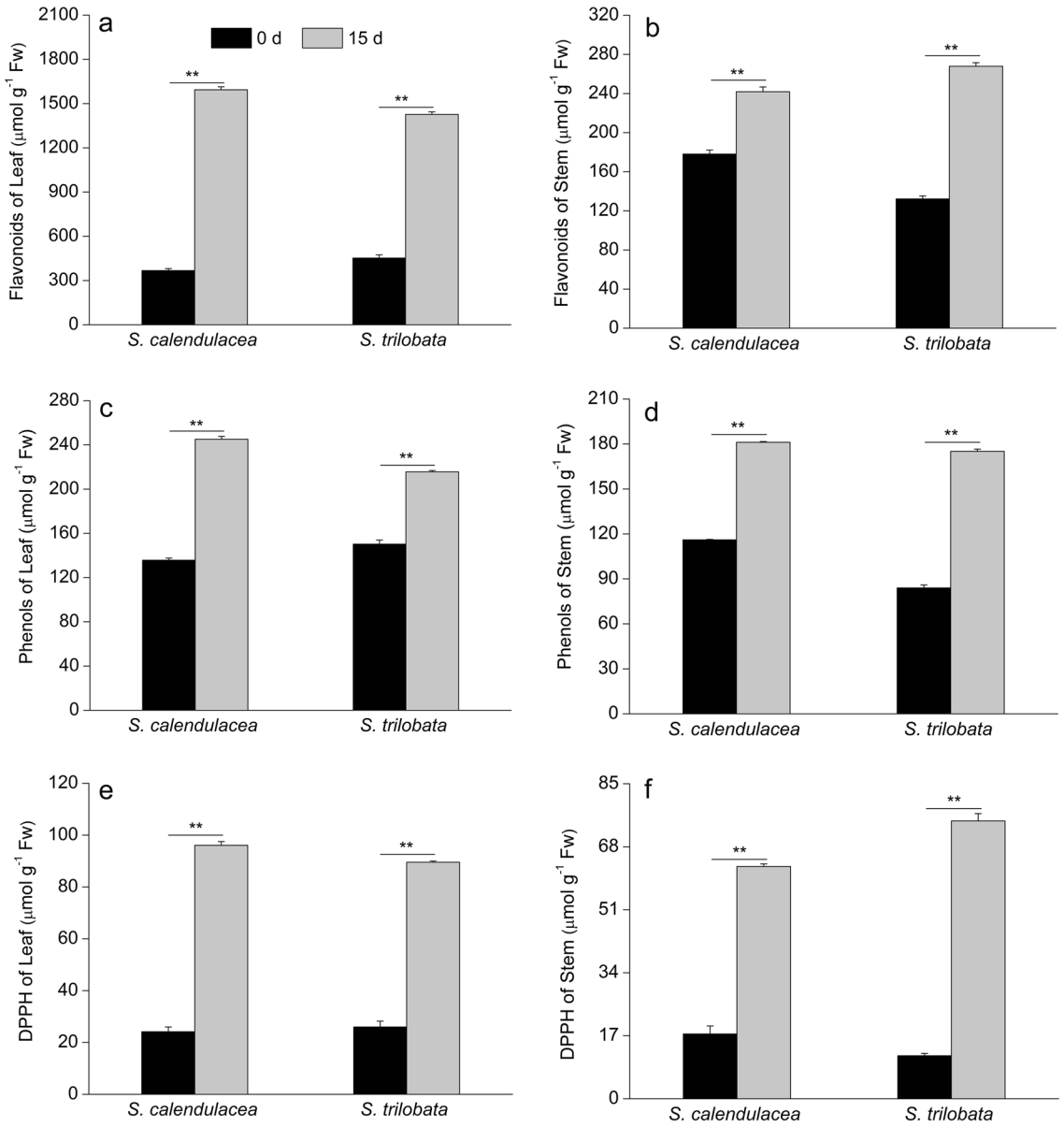

Fig. 5 Changes in antioxidant substance contents in the leaves and stems of two *Sphagneticola* species under low temperatures. Panels **a** and **b** show the changes in flavonoid content in the leaves and stems of the two *Sphagneticola* species. Panels **c** and **d** show the changes in total phenol content in the leaves and stems of the two *Sphagneticola* species. Panels **e** and **f** show the changes in total antioxidant capacity in the leaves and stems, respectively ($n=5$). **indicates an extremely significant difference between 0 and 15 days after low-temperature treatment ($p<0.01$)

a consistent trend. The percent increase in relative membrane leakage in the defoliated stem of *S. trilobata* was only approximately 1/11 that in the native plant stems (Fig. 7b).

Changes in the basic indicators in the intact and defoliated stems.

In this study, we further measured the basic physiological indicators of the stem. The results showed that the diameter and total biomass of the stem increased in both *Sphagneticola* species compared to those at the start of treatment. The defoliated stem diameters of *S. trilobata* and *S. calendulacea* increased by 10.38% and 8.32%, respectively (Fig. 8a). The percent increase in the total biomass of *S. trilobata* was more than 13 times that of *S. calendulacea* (Fig. 8b).

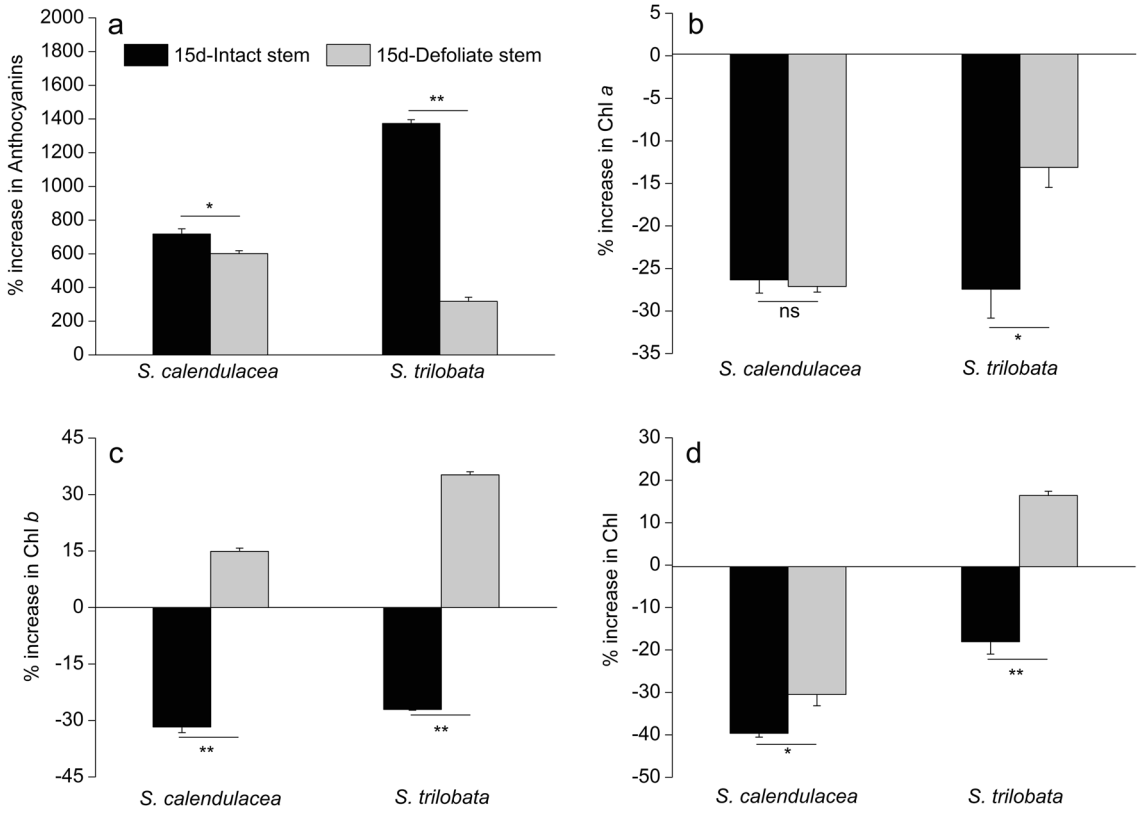

Fig. 6 The % increase in anthocyanin and photosynthetic pigments in the intact and defoliated stems of two *Sphagneticola* species under low temperature. Panel **a** represents the % increase in anthocyanin in stems after 15-day low-temperature treatment compared to that at 0 day. Panel **b** represents the % increase in Chl *a* in stems after 15 days of low-temperature treatment compared to that at 0 day. Panel **c** represents the % increase in Chl *b* in stems after 15 days of low-temperature treatment compared to that at 0 day. Panel **d** shows the % increase in Chl in stems after 15 days of low-temperature treatment compared to that at 0 day. * indicates a significant difference between intact and defoliated stems after low-temperature treatment ($0.01 < p < 0.05$); ** indicates an extremely significant difference between intact and defoliated stems after low-temperature treatment ($p < 0.01$) ($n = 5$)

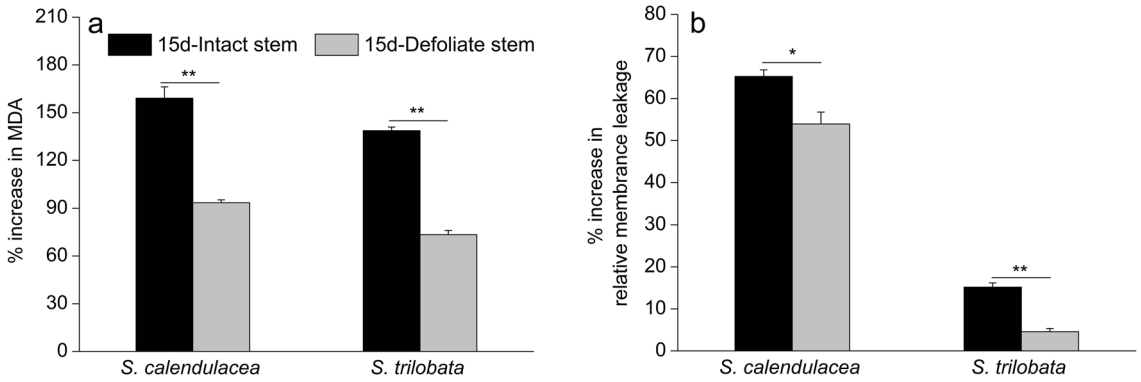

Fig. 7 The % increase in the properties of cell membranes in intact and defoliated stems of two *Sphagneticola* species at low temperatures. Panel **a** represents the % increase in Malondialdehyde (MDA) in the stems, and Panel **b** represents the % increase in cell membrane leakage in the stems of the two *Sphagneticola* species after 15-day low-temperature treatment compared to that at 0 day. *Indicates a significant difference between intact and defoliated stems after low-temperature treatment ($0.01 < p < 0.05$); **Indicates an extremely significant difference between intact and defoliated stems after low-temperature treatment ($p < 0.01$) ($n = 5$)

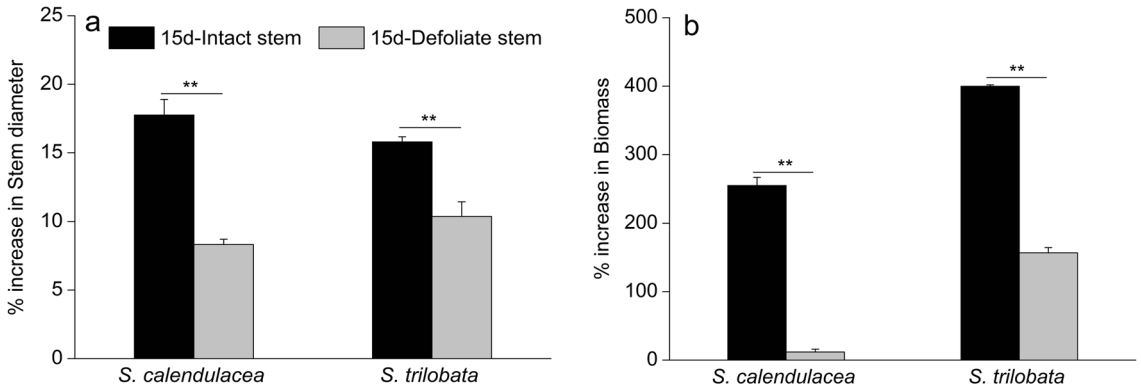

Fig. 8 The % increase in diameter and biomass in the intact and defoliated stems from two *Sphagneticola* species at low temperature. Panel **a** represents the % increase in the diameter of stems, and Panel **b** represents the % increase in the biomass of stems after 15-day low-temperature treatment compared to that at 0 day. *indicates a significant difference between intact and defoliated stems after low-temperature treatment ($0.01 < p < 0.05$); **indicates an extremely significant difference between intact and defoliated stems after low-temperature treatment ($p < 0.01$) ($n = 5$)

Discussion

Leaves are the primary photosynthetic organs, and their phenotypic plasticity has been the focus of most research on the mechanisms by which invasive plants adapt to the external environment. The stem, as a non-photosynthetic organ, also plays a major role in the process of plant invasion, but little research has been performed on its phenotypic plasticity. Since *S. trilobata* is one of the main invasive plants in South China, we used this experimental material as well as a native *Sphagneticola* species to study the role of the stem in phenotypic plasticity under low temperature, and proposed a regulatory mechanism of the redistribution of energy resources among organs to explain a possible additional mechanism that enhances invasiveness.

Stems of *S. trilobata* have a stronger tolerance under low temperature

Temperature is a major factor that limits the normal growth and development of plants. In this study, it was found that the leaves of *S. calendulacea* had stronger low-temperature tolerance than those of *S. trilobata* leaves. The *S. calendulacea* leaves did not show obvious damage, but *S. trilobata* leaves had large areas of yellowing and low tolerance to low temperature. By contrast, *S. trilobata* stems showed higher tolerance to low temperatures than *S. calendulacea* (Fig. 1).

The anthocyanin contents in the stems of the two plant species increased significantly under the low-temperature treatment (Fig. 2b). The stem epidermis of *S. trilobata* showed a more obvious increase in reddening than that of *S. calendulacea* (Fig. 1). Low temperature can cause anthocyanin accumulation, as reported in various studies (Zhang et al. 2019). The production of anthocyanins can attenuate external light energy somewhat and can reduce the accumulation of excess light energy (Zhang et al. 2016). Our results indicate that the stem of *S. trilobata* had a greater screening effect on external light energy at low temperatures and could better reduce the accumulation of excess light energy.

In numerous studies, it was found that the increase in anthocyanin content was often accompanied by a decrease in chlorophyll in adverse environmental conditions (Yuan et al. 2013), which prompts the question of whether there is a negative correlation between the two. At present, the literature is unclear on this question, so this phenomenon needs to be studied further. Consistent with the results of previous studies, the photosynthetic pigments, including Chl *a*, Chl *b*, and Chl, in the stem of *S. trilobata* showed a consistent change trend (Fig. 2d, f, h). The content of photosynthetic pigments in the stem of *S. trilobata* decreased significantly at low temperature, but the decrease was smaller than that in *S. calendulacea*. This indicated that low temperature might affect photosynthetic pigment synthesis (Glaszmann et al. 1990), but the degree of inhibition of pigment synthesis was lower in *S. trilobata* than in the native species. Studies have found that chlorophyll fluorescence kinetic parameters can reflect photosynthetic ability of plants (Fu et al. 2012). F_v/F_m is the most commonly used fluorescence parameter, indicating the maximum photochemical efficiency of PSII. When plants are grown in non-adverse conditions, the range of this parameter is generally 0.75–0.85, but it decreases significantly with adversity or damage (Maxwell and Johnson 2000). The F_v/F_m of the stems of the two *Sphagneticola* species had the same downward trend, and the decline rate of *S. calendulacea* was larger than that of *S. trilobata* (Fig. 3b). The Φ_{PSII} (Fig. 3d) and ETR (Fig. 3f) of the stems exhibited the same decreasing trend as did the F_v/F_m. The results indicated that low temperature may damage the photosynthetic

structure, inhibit photosynthetic electron transport, and lead to a decline in photosynthetic capacity (Ojeda-Pérez et al. 2017).

In general, the decrease in photosynthetic capacity under low temperature leads to excess light energy and the accumulation of ROS (Ksas et al. 2015; Zhang et al. 2012a, b; Lee et al. 2004). Similarly, the results of the tissue localization of ROS showed that the accumulation of superoxide anions (Fig. 4a) and hydrogen peroxide (Fig. 4b) in the stem of *S. trilobata* was lower than that in the native plant stems. It also indicated that the photosynthetic capacity was higher and the extent of photoinhibition was lower in *S. trilobata* than in the native plant.

Interestingly, the opposite results were found in the leaves of the two plants. At low temperature, the leaves of *S. trilobata* showed yellowing (Fig. 1), increased anthocyanin content (Fig. 2a), decreased chlorophyll content, and lower external light absorption capacity than that of the native plant (Fig. 2c,e,g), as well as a larger decrease in the chlorophyll fluorescence kinetic parameters of the leaves, including F_v/F_m, Φ_{PSII}, ETR (Fig. 3a, c, e). These results indicated that the photosynthetic capacity of the leaves of the invasive plants decreased greatly, resulting in serious excess light energy and ROS accumulation in the *S. trilobata* leaves than in the *S. calendulacea* leaves (Fig. 4a, b). Therefore, the stress on the leaves of *S. trilobata* was greater than that on the native plant leaves at low temperature. This is consistent with the findings of Wu et al. (2013) that the main distribution areas of *S. calendulacea* were in the temperate zone. Sun et al. (2015) also found that under extremely low-temperature conditions, leaf wilting in *S. trilobata* was more severe.

ROS in plants exist in a dynamic equilibrium state (Mhamdi and Van Breusegem 2018). Some studies have demonstrated that excessive production of ROS can overwhelm the scavenging system and that antioxidants can effectively scavenge and maintain the balance of ROS (Poljsak et al. 2013; Caverzan et al. 2016). In this study, we found that the increase in antioxidant substances, including flavonoids and total phenols, produced in the stem of *S. trilobata* was greater than that of the native species stem (Fig. 5b, d). The increase in antioxidative substances in the leaves of *S. trilobata* was smaller than that in the native plant (Fig. 5a, c). That is, *S. trilobata* had a stronger total antioxidant capacity in the stem (Fig. 5f), while *S. calendulacea* had a stronger total antioxidant capacity in the leaves (Fig. 5e). The differential location of the main antioxidant capacity in the two species also explains the reason that under the same low-temperature conditions, the accumulation of ROS in the stem of *S. trilobata* was small, while that in the leaves of native plant was small. These increased antioxidants could effectively remove the accumulated reactive oxygen species at low temperature.

Therefore, these results indicate that the tolerance of different organs of the same plant to low temperatures will have a combined effect; if the anthocyanin content and antioxidant synthesis of the stem could be increased, the total antioxidant capacity could be improved, the accumulation of reactive oxygen species could be effectively eliminated, and the damage to cell membrane integrity could be reduced in the same plant when the leaves were insufficiently photoprotected. There appears to be a strategy of resource redistribution, which could transfer more newly synthesized resources to the stems for improving the photosynthetic capacity of stems, thereby compensating for the loss of the leaves as photosynthetic organs.

Stem of *S. trilobata* has a compensatory effect under low temperatures

At present, many invasive plants have been reported to possess a compensatory mechanism for resource redistribution among different organs (Thapa et al. 2018). Invasive plants are believed to be more regenerative and compensatory than native plants, which is one of the principal reasons for their invasiveness. In this study, a defoliation experiment was used to further verify whether there was a compensatory effect in the stem of *S. trilobata* under low temperature. The results showed that after defoliation, the stem showed reduced anthocyanin synthesis (Fig. 6a) and reduced redness (Fig. 1), but increased chlorophyll content (Fig. 6b, c, d). These changes ensure that *S. trilobata* stem with defoliation could absorb more light for photosynthesis than that of *S. calendulacea.* Therefore, the defoliation treatment caused the stem of *S. trilobata* to acclimate and acquire a higher photosynthetic compensation capability. Some studies have also shown that the improvement of photosynthesis is a compensatory mechanism in plants and that defoliation can change the photosynthetic status of organs from source to sink and vice versa, thus affecting the possibility of compensatory photosynthesis (Ida et al. 2012).

Compared to that in the intact stem, the degree of oxidative stress in the stem caused by low temperature appears to have been alleviated after defoliation, since the degree of membrane lipid peroxidation (Fig. 7a) and cell membrane leakage decreased (Fig. 7b). This was mainly due to the improvement in the photosynthetic capacity of stems after defoliation. Therefore, the compensatory improvement of the photosynthetic capacity of stems after defoliation was also conducive to the storage of more nutrients in stems, ensuring that the stem diameter (Fig. 8a) and biomass (Fig. 8b) of the two *Sphagneticola* species increased at low temperature. These results indicated that the stems of the two *Sphagneticola* species showed a certain photosynthetic compensatory effect that could partly compensate for the loss of the photosynthetic organ leaves after defoliation. The

stem photosynthetic compensation and resource allocation ability of *S. trilobata* were better than those of *S. calendulacea*. This is also in line with results indicating that invasive plants still produce higher biomass than native plants after defoliation (Burns et al. 2007).

In summary, the resource redistribution between the leaves and stem gives the stem a stronger compensatory effect at low temperatures. This strategy would favor *S. trilobata*, which mainly uses clonal reproduction to maintain normal reproduction throughout the year, accelerating its invasion and affecting its distribution in South China. The stem was more tolerant under low temperatures, which could also promote the invasion of temperate areas by *S. trilobata*.

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Author contributions Minling Cai carried out the experiments, analyzed the data, and the drafted the whole manuscript. Wenqiao Ding and Junjie Zhai participated in the experiments. Wenqiao Ding and Xiaoting Zheng participated in the preparation of the Figures. Zhengchao Yu, Qilei Zhang, and Xiaohua Lin contributed to sample collection. Wah Soon Chow modified the grammar and checked the form of manuscript. Changlian Peng designed the research and experiments.

Data availability All datasets for this study are included in the manuscript and/or the Supplementary Files.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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