PHOTOSYNTHETICA
International Journal for Photosynthesis Research

DOI 10.32615/ps.2023.011 PHOTOSYNTHETICA 61 (1): 115-123, 2023

The physiological responses of critically endangered species *Ardisia gigantifolia* Stapf (Primulaceae) to different light intensities

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Abstract

To investigate the light intensity suitable for the growth of *Ardisia gigantifolia* Stapf, morphology, photosynthetic parameters, and indicators of oxidative stress were analyzed under different light intensities. Compared to high-irradiance treatment, medium and low-irradiance treatments promoted plant growth and restricted transpiration. Compared to medium irradiance, plants under high and low irradiance exhibited significantly lower maximal photochemical efficiency, potential photochemical efficiency, and electron transport rate, but significantly higher malondialdehyde content. This indicated that both excessive light and severe shading inhibited photosynthetic activity and induced oxidative stress, which resulted in a significant decrease in net photosynthetic rate. *A. gigantifolia* can adapt to different light intensities, improving light harvesting and utilizing capacity under low irradiance by increasing Chl (*a*+*b*) content and reducing Chl *a*/*b* ratio, and adapting to high irradiance by enhancing heat dissipation and activity of peroxidase. *A. gigantifolia* showed the best performance in growth and photosynthesis under medium irradiance treatment.

Keywords: light deficiency; oxidative stress; photoinhibition; photosynthesis.

Introduction

Light provides a source of energy for light reactions of photosynthesis. All plants have their optimal light intensity ranges for growth because excessive high and low irradiances would result in photoinhibition and light deficiency, respectively (Berry 1982, Deng *et al.* 2012, Shao *et al.* 2014). Plants could adapt to varying light conditions through morphological and physiological regulation (Deng *et al.* 2012, Shao *et al.* 2014, Lee *et al.* 2021). Photosynthetic parameters, chlorophyll (Chl) fluorescence, Chl content, and indicators of oxidative stress are commonly used to investigate the physiological regulation of plants in varying light conditions.

Compared to the full sunlight conditions, shade increased the photosynthetic rate of shade-tolerant species, such as *Anoectochilus roxburghii* and *Bletilla ochracea* (Shao *et al.* 2014, Yu *et al.* 2022). Shade resulted in the

Highlights

- Medium irradiance was the optimum light intensity for growth and photosynthesis in *Ardisia gigantifolia*
- High and low irradiance inhibited photosynthesis in *A. gigantifolia*
- *A. gigantifolia* adapted to excessive irradiance and light deficiency through physiological regulation

Received 29 December 2022
Accepted 21 March 2023
Published online 11 April 2023

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Abbreviations: *E* – transpiration rate; ETR – electron transport rate; F_0 – minimal fluorescence yield of the dark-adapted state; F_m – maximum fluorescence yield of the dark-adapted state; F_v/F_0 – potential photochemical efficiency; F_v/F_m – maximal quantum yield of PSII photochemistry; MDA – malondialdehyde; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; POD – peroxidase; q_P – photochemical quenching coefficient.

Acknowledgments: This work was financially supported by the Natural Science Foundation of Guangdong Province (grant no. 2022A1515010904), and the Guangdong Provincial Key R&D Program (grant no. 2022B1111040003). We thank Xingyun Liang for providing a photosynthesis measuring system for this study, and anonymous reviewers for valuable suggestions that greatly improved the paper.

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

increase of Chl (*a*+*b*) content and the decrease of Chl *a*/*b* ratio of shade-tolerant species, such as *Ardisia violacea* and *Festuca arundinacea* (Zhang *et al.* 2014, De *et al.* 2015, Yu *et al.* 2022). Chl fluorescence parameters effectively reflect the internal photosystem performance of plants in stressful environments by measuring light absorption, transmission, dissipation, and distribution in photosynthesis (Chen *et al.* 2006, Alyemeni *et al.* 2018). F_v/F_m (maximal quantum yield of PSII photochemistry) can reflect the light energy conversion efficiency and the efficiency of excitation capture of PSII reaction centers (Kitajima and Butler 1975). F_v/F_0 (potential photochemical efficiency) is an indicator of the energy-utilization capability of plants. Higher F_v/F_m and F_v/F_0 mean the greater light energy utilization potential of plants (Maxwell and Johnson 2000). ETR (electron transport rate) is associated with the photosynthetic rate of plants (Baker 2008). Photochemical quenching (q_P) is an indicator of the proportion of opened PSII reaction centers, and a high q_P is beneficial to the quantum yield and electron transport in the PSII centers (Maxwell and Johnson 2000, Baker 2008). NPQ reflects the redundant light energy dissipated harmlessly as heat energy, which is beneficial to reduce the damage caused by photoinhibition (Müller *et al.* 2001, Baker 2008). Shade-tolerant species *B. ochracea* suffered from photoinhibition under full sunlight conditions, in which plants exhibited significantly lower values of F_v/F_m, F_v/F_0, ETR, and q_P, while a significantly higher value of NPQ (Yu *et al.* 2022).

Abiotic stress induces plants to suffer oxidative stress (Fu *et al.* 2000, 2012). MDA (malondialdehyde) is the product of cell membrane lipid peroxidation, and its content increases with the deepening of stress (Shah *et al.* 2001, Sharma and Dubey 2007). Responses of MDA content to shading depend on plant species. Shade significantly increased the MDA content of shade-intolerant rice hybrid (Liu *et al.* 2012) but decreased the MDA content of shade-tolerant species *A. roxburghii* (Shao *et al.* 2014). PODs (peroxidases) are important protective enzymes in the antioxidant enzyme system (Shah *et al.* 2001). Light intensity has a substantial impact on turning the POD activity (Li *et al.* 2016, Yi *et al.* 2020).

Ardisia gigantifolia Stapf (Primulaceae) is a critically endangered subshrub endemic to the Yunnan Province of China (Qin *et al.* 2017) and its scientific name has long been confused with the Chinese medicinal plant 'Zou Ma Tai' (Huang *et al.* 2017). Most species in *Ardisia* are used for medicinal purposes, suggesting that *A. gigantifolia* would have potential medicinal value (Liu *et al.* 2018). Besides, *A. gigantifolia* has high ornamental value for its compact plant shape, big leaves, long flowering period, and large number of pink flowers. Despite the endangered state, and high medicinal and ornamental value of *A. gigantifolia*, there is little research on this species, especially its adaption to the environment, since it was described in 1906.

A. gigantifolia grows under dense evergreen broad-leaved forests in the wild, so light intensity would be a dominant ecological factor affecting the survival of this species. It is necessary to investigate the light intensity suitable for *A. gigantifolia* and its adaption to different light intensities, which contributes to maximizing its economic, medicinal, and ornamental value. For these purposes, the morphological parameters, photosynthesis, chlorophyll fluorescence, chlorophyll content, and indicators of oxidative stress were investigated in *A. gigantifolia* under different light intensities. The results of this study can provide a reference for the conservation and utilization of *A. gigantifolia*.

Materials and methods

Plant materials and growth conditions: Wild plants of *A. gigantifolia* were collected in Nanxi town of Hekou County, Yunnan Province (23°11'N, 113°22'E), and maintained in a greenhouse at the South China Botanical Garden, China (22°37'N, 103°57'E). Plants of *A. gigantifolia* used in this study were tissue culture plantlets derived from leaves. All plants were grown in 21-cm plastic pots filled with a 3:1 (v:v) mixture of peat soil and perlite. One seedling per pot was grown. The pots were irrigated twice a week and fertilized with 2 g of slow-released compound fertilizer (nitrogen content of 18%) twice a year.

Experiment design: The six-month-old seedlings with no disease and insect pests were divided into three groups for each shade treatment. At the beginning of the experiment, there was no significant difference in morphology of

Fig. 1. The appearance of *Ardisia gigantifolia* after 24 months of different shade treatments.

the seedlings, and the initial plant height of these seedlings was 20–22 cm. Plants of *A. gigantifolia* were subjected to three shade treatments for 24 months, beginning on 4 September 2020. Each treatment involved 30 plants (Fig. 1).

Treatments consisted of high, medium, and low irradiance treatments. The relative irradiance in each treatment was determined using the illuminometer (*SW-582*, *SNDWAY*, China). Diurnal variation of light intensities under the three treatments and the full sunlight conditions were measured using the illuminometer at a fixed horizontal position above the plant on an overcast day (Fig. 2). The ratio of light intensity under a treatment to the light intensity under full light was caculated at each time point of a day. For a treatment, the average value of the ratio during a day was reported as the relative irradiance of the treatment.

Treatment	Transmittance [%]	Relative irradiance [%]
High irradiance (H)	81.20–86.17	83.1
Medium irradiance (M)	30.49–33.92	32.0
Low irradiance (L)	12.72–15.41	14.4

Different types of spectrally neutral black sunshade nets were used to provide shade to *A. gigantifolia* at a greenhouse. A high (83.1%) irradiance condition was reached without any shading because the light transmittance of the greenhouse was approximately 83.1%. The medium (32.0%) irradiance condition was reached using a layer of sunshade net with 6-pin encryption and the low (14.4%) irradiance was reached using a layer of the net with 8-spin encryption. The height of the shed nets was 1.5 m and the distance between each pot was 50 cm to avoid cross shade. During the experiments, all plants were supplied with the same water and fertilizer management and were protected from bacterial pathogens and weed competition.

Morphological parameters: Measurements of plant height, leaf length, and leaf width were performed after 24 months of shade treatments. Ten plants were randomly selected in each treatment group. The first or the second leaf from the top down was selected to measure leaf length and leaf width. Plant height refers to the vertical distance from the plant base to the leaf tip. Each sample was measured three times in parallel.

Photosynthetic parameters and Chl fluorescence: Photosynthetic parameters and Chl fluorescence were measured using the photosynthesis measuring system (*LI-6800*, *LI-COR*, USA). After 24 months of shade treatments, data were recorded between 8:30 and 11:30 h on sunny days. Photosynthetic parameters included net photosynthetic rate [μmol(CO_2) m^{-2} s^{-1}] and transpiration rate [μmol(H_2O) m^{-2} s^{-1}]. Air cuvette irradiance, temperature, and CO_2 concentration in the leaf chamber were maintained at 800 μmol(photon) m^{-2} s^{-1}, 28°C, and 400 μmol mol^{-1}, respectively. The data of photosynthetic parameters were recorded following a 10-min acclimation period. Five plants were randomly selected to measure photosynthetic parameters in each treatment group.

Leaves were dark-adapted for a night (about 14 h) before measurements of minimal fluorescence yield (F_0) and maximum fluorescence yield of the dark-adapted state (F_m). The maximal quantum yield of PSII photochemistry (F_v/F_m) and potential photochemical efficiency (F_v/F_0) were calculated based on methods reported earlier: $F_v/F_m = (F_m - F_0)/F_m$, $F_v/F_0 = (F_m - F_0)/F_0$ (Fu *et al.* 2012, Li *et al.* 2015). Leaves were light-adapted at the respective growth irradiance for approximately 30 min before the measurements of photochemical [$q_P = (F_m' - F_s)/(F_m' - F_0')$] and nonphotochemical [$NPQ = (F_m - F_m')/F_m'$] quenching parameters of Chl fluorescence, the effective quantum yield of photochemical energy conversion [Yield = $(F_m' - F_s)/F_m'$], the electron transport rate through PSII (ETR = 0.5 × α × PAR × Yield, [μmol m^{-2} s^{-1}]) (Maxwell and Johnson 2000). The photosynthetically active radiation (PAR) of high, medium, and low irradiance conditions were about 51, 24, and 11 μmol(photon) m^{-2} s^{-1} during the measurement of light-adapted Chl fluorescence parameters. Temperature and CO_2 concentration were maintained at 28°C and 400 μmol mol^{-1}, respectively.

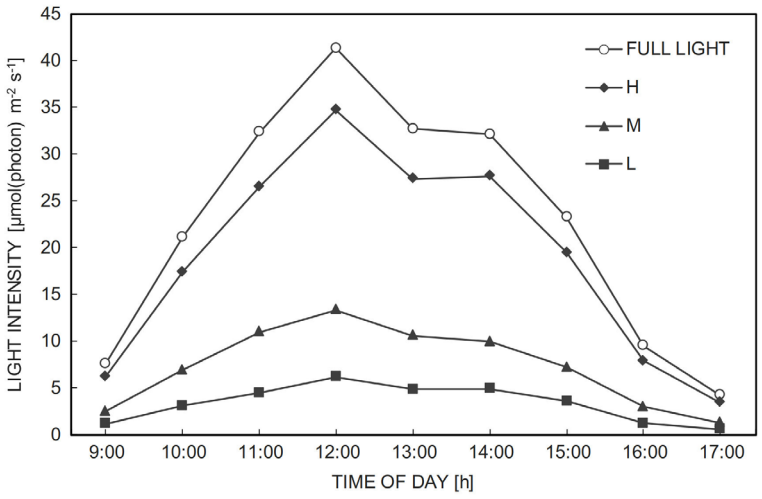

Fig. 2. Diurnal variation of light intensity [μmol(photon) m^{-2} s^{-1}] at a fixed horizontal position above the plant under full sunlight conditions and the three different shade treatments on an overcast day. H – high irradiance; M – medium irradiance; L – low irradiance.

The first or the second leaf from the top down was selected to measure the photosynthetic characteristics and Chl fluorescence of each plant. Three plants were randomly selected to measure Chl fluorescence in each treatment group.

Chl contents: The three leaves used for the measurement of Chl fluorescence were collected from each treatment for determination of Chl content [Chl *a*, Chl *b*, Chl (*a*+*b*)] and the ratio of Chl *a*/*b*. Chl pigments were extracted by grinding leaves in 80% acetone in the dark at room temperature, with their concentrations expressed as mg g^{-1}(DM) based on the equations of Porra (2002).

Indicators of oxidative stress: Three healthy leaves of similar ages from three plants were collected from each treatment to measure the indicators of oxidative stress. Malondialdehyde (MDA) content was measured by the thiobarbituric acid method to determine the accumulation of lipid peroxide in tissues (Stewart and Bewley 1980). The activity of peroxidase (POD, EC 1.11.1.7, [U mg^{-1}(protein)]) was analyzed following the change of absorbance at 470 nm due to guaiacol oxidation, and was assayed according to Doerge *et al.* (1997).

Statistical analysis: Data were subjected to one-way analysis of variance (*ANOVA*) using statistical software *SPSS 20.0* (*SPSS*, Chicago, IL, USA). A significant level of 0.05 was used for all statistical tests by *Duncan*'s multiple range test. Correlations between measured parameters were analyzed by *Pearson*'s correlation test using *SPSS 20.0*.

Results

Growth parameters: After 24 months of shade treatments, the plants of *A. gigantifolia* under medium (32.0%) and low (14.4%) irradiance had significantly higher plant height, leaf length, and width than plants under high (83.1%) irradiance (Fig. 3). Plants under medium irradiance exhibited higher plant height, leaf length, and width than plants under low irradiance, but the differences were not significant (Fig. 3).

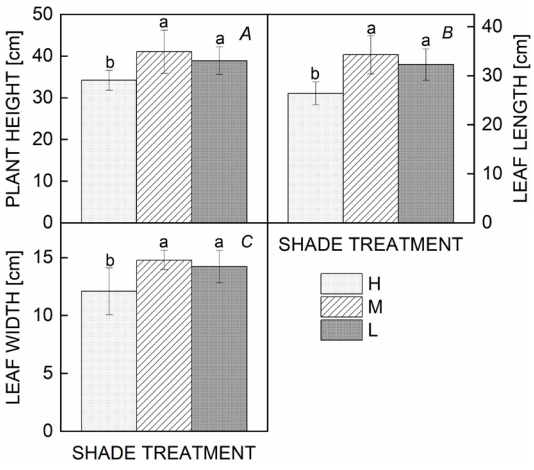

Fig. 3. Morphological parameters of *Ardisia gigantifolia* under different shade treatments. The parameters included plant height (*A*), leaf length (*B*), and leaf width (*C*). The data are expressed as mean ± SD (n = 10). *Different letters* indicate significant differences between shade treatments (P<0.05). H – high (83.1%) irradiance; M – medium (32.0%) irradiance; L – low (14.4%) irradiance.

Photosynthetic parameters: The highest value of P_N was observed under medium irradiance and the lowest under low irradiance (Fig. 4). There were significant differences in the value of P_N between the shade treatments; the value of P_N was in the order of medium irradiance > high irradiance > low irradiance (Fig. 4). The values of E decreased significantly with the increase of shading, and they were in the order of high irradiance > medium irradiance > low irradiance (Fig. 4).

Chl fluorescence: After a night of dark acclimation, the highest value of F_v/F_m and F_v/F_0 were observed in plants under medium irradiance (Fig. 5*A*,*B*). Plants under medium irradiance exhibited significantly higher F_v/F_m and F_v/F_0 than that of plants under high and low irradiance (Fig. 5*A*,*B*). However, there was no significant difference in F_v/F_m and F_v/F_0 between plants under high and low irradiance (Fig. 5*A*,*B*).

After 30 min of light adaption, the highest values of ETR and q_P were observed under medium irradiance and the lowest under high irradiance (Fig. 5*C*,*E*). The differences in ETR were significant between the three treatments (Fig. 5*C*). The values of q_P differed significantly between medium and high irradiance, while there was no significant difference in q_P between medium and low irradiance (Fig. 5*E*). Plants in high irradiance exhibited a significantly higher value of NPQ than medium and low irradiance, while the value of NPQ did not differ significantly between medium and low irradiance (Fig. 5*D*).

Chl contents: The contents of Chl *a*, Chl *b*, and Chl (*a*+*b*) increased significantly with the increase of shading,

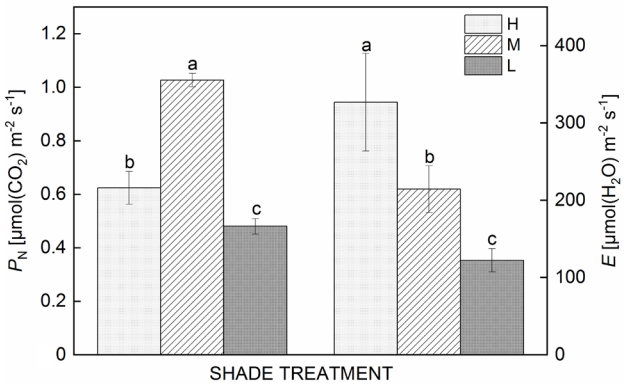

Fig. 4. Net photosynthetic rate (P_N) and transpiration rate (E) of *Ardisia gigantifolia* under different shade treatments. The values represented mean ± SD (n = 5). *Different letters* indicate significant differences between shade treatments (P<0.05). H – high (83.1%) irradiance; M – medium (32.0%) irradiance; L – low (14.4%) irradiance.

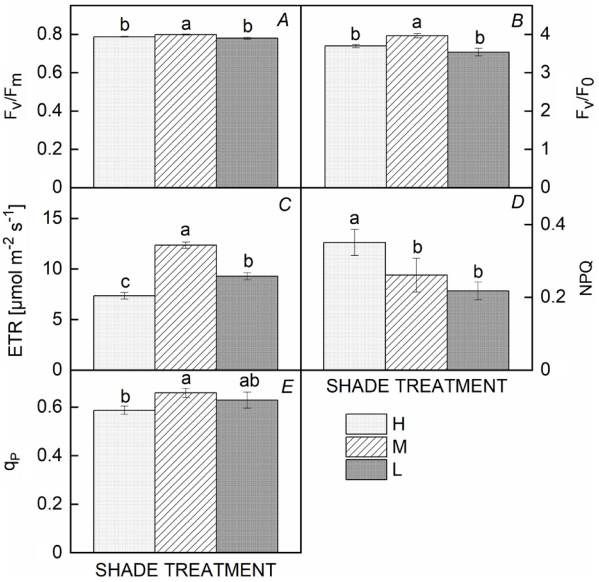

Fig. 5. Chlorophyll fluorescence parameters of *Ardisia gigantifolia* under different shade treatments. The parameters included maximal quantum yield of PSII photochemistry (F_v/F_m) (*A*), potential photochemical efficiency (F_v/F_0) (*B*) measured after a dark adaption, and electron transport rate (ETR) (*C*), nonphotochemical quenching (NPQ) (*D*), photochemical quenching coefficient (q_P) (*E*) measured after light adaption. The values represented mean ± SD (n = 3). *Different letters* indicate significant differences between shade treatments (P<0.05). H – high (83.1%) irradiance; M – medium (32.0%) irradiance; L – low (14.4%) irradiance.

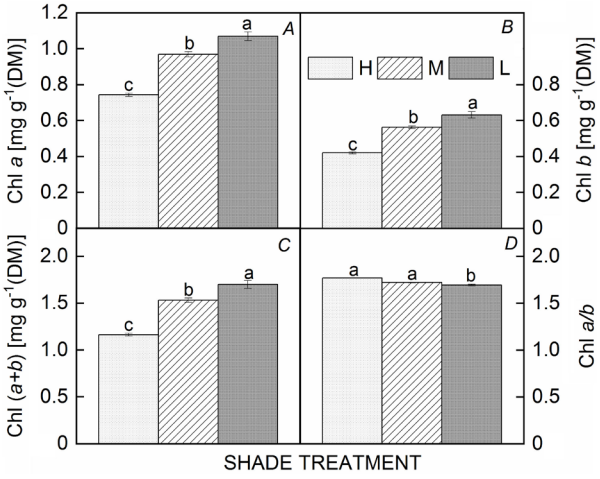

Fig. 6. The content of Chl *a* (*A*), Chl *b* (*B*), Chl (*a*+*b*) (*C*), and the Chl *a*/*b* (*D*) ratio of *Ardisia gigantifolia* under different shade treatments. The values represented mean ± SD (n = 3). *Different letters* indicate significant differences between shade treatments (P<0.05). H – high (83.1%) irradiance; M – medium (32.0%) irradiance; L – low (14.4%) irradiance.

which was in the order of low irradiance > medium irradiance > high irradiance (Fig. 6). In contrast, the ratio of Chl *a*/*b* decreased with the increase of shading, which was in the order of high irradiance > medium irradiance > low irradiance (Fig. 6*D*). There was a significant difference in Chl *a*/*b* ratio between medium and low irradiance (Fig. 6*D*), while there was no significant difference in Chl *a*/*b* ratio between high and medium irradiance (Fig. 6*D*).

Indicators of oxidative stress: The MDA content differed significantly between the three shade treatments, and they were in order of high irradiance > low irradiance > medium irradiance (Fig. 7). The value of POD activity was in the order of high irradiance > low irradiance > medium irradiance, which was similar to the order of MDA content (Fig. 7). Plants under high irradiance exhibited a significantly higher value of POD activity than that of plants under medium and low irradiance (Fig. 7), while the difference in POD activity was not significant between medium and low irradiance (Fig. 7).

The relationships between measured parameters under different treatments: Under the three treatments, plants did not show significant correlations between P_N and plant height, leaf width, F_v/F_m, ETR, q_P, Chl *a* and Chl *b* content, MDA content, POD activity (Fig. 8*A–C*). The correlation between P_N and leaf length was significant under medium and low irradiance (Fig. 8*A*), while the correlation was insignificant under high irradiance (Fig. 8*A*). The correlation between P_N and leaf length was significantly positive under medium irradiance but markedly negative under low irradiance (Fig. 8*A*). Plants under high irradiance exhibited a significantly negative correlation between P_N and NPQ (Fig. 8*B*), but the correlation was insignificant under medium and low irradiance (Fig. 8*B*). There was no significant correlation between F_v/F_m and Chl *a*, Chl *b*, POD activity under the three treatments (Fig. 8*D*). Plants under high and low irradiance showed a significantly negative correlation

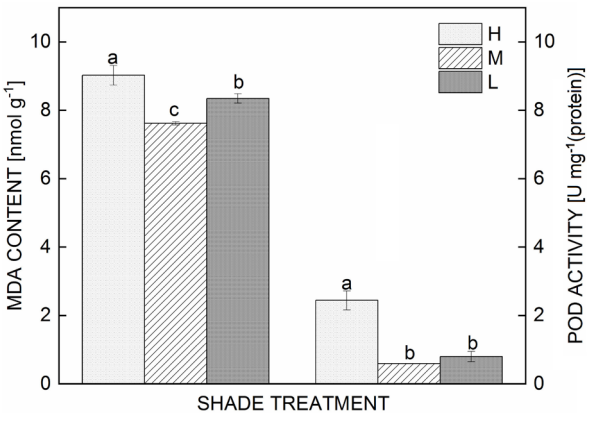

Fig. 7. Malondialdehyde (MDA) content and peroxidase (POD) activity of *Ardisia gigantifolia* under different shade treatments. The values represented mean ± SD (n = 3). *Different letters* indicate significant differences between shade treatments (P<0.05). H – high (83.1%) irradiance; M – medium (32.0%) irradiance; L – low (14.4%) irradiance.

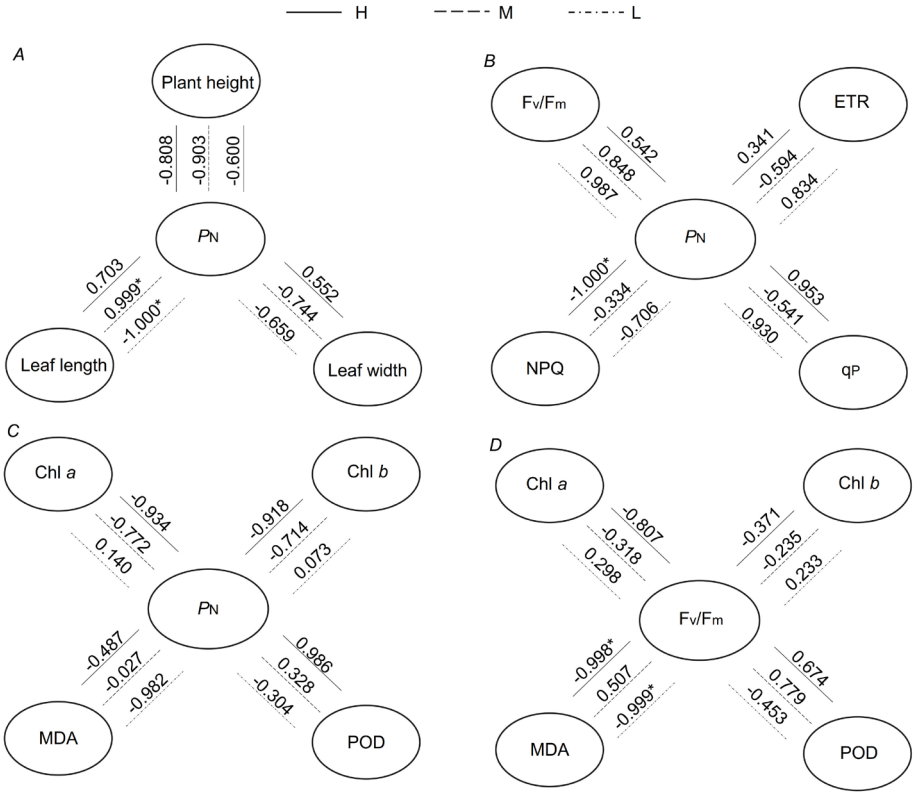

Fig. 8. Correlation coefficients (*r*) between net photosynthetic rate (P_N) and morphological parameters (*A*), chlorophyll fluorescence parameters (*B*), Chls (Chl *a* and Chl *b*) content, malondialdehyde (MDA) content, and peroxidase (POD) activity (*C*), as well as correlation coefficients (*r*) between the maximal quantum yield of PSII photochemistry (F_v/F_m) and Chls (Chl *a* and Chl *b*) content, MDA content, and POD activity (*D*). Morphological parameters included plant height, leaf length, and leaf width. Chlorophyll fluorescence parameters included F_v/F_m, electron transport rate (ETR), nonphotochemical quenching (NPQ), and photochemical quenching coefficient (q_P). Asterisk superscript represents significant correlations (P<0.05). H – high (83.1%) irradiance; M – medium (32.0%) irradiance; L – low (14.4%) irradiance.

between F_v/F_m and MDA (Fig. 8*D*), while the correlation was insignificant under medium irradiance (Fig. 8*D*).

Discussion

Morphological and photosynthetic responses to different light intensities: The morphological and photosynthetic characteristics reflect the ability of plants to survive and grow in different environments (Gao *et al.* 2019). Plants under high (83.1%) irradiance exhibited significantly lower plant height, leaf length, leaf width, and P_N than plants under medium (32.0%) and low (14.4%) irradiance (Figs. 3, 4). Excessive irradiance has been reported to cause photoinhibition and a decrease in PSII activity (Shao *et al.* 2014, Liu *et al.* 2019, Yang *et al.* 2019), which would result in the inhibition of photosynthesis and growth of *A. gigantifolia* under high irradiance. Plants under medium irradiance presented the highest values of the three morphological parameters and P_N, indicating that moderate irradiance can improve the growth and photosynthesis of *A. gigantifolia*. The possible reason could be that moderate shade can decrease photoinhibition and improve the utilization rate of light energy (Chen *et al.* 2017, Liu *et al.* 2019). However, plants under low (14.4%) irradiance showed significantly lower P_N than plants under high and medium irradiance (Fig. 3), similar to *A. roxburghii* and *Eleutherococcus senticosus* (Shao *et al.* 2014, Xu *et al.* 2020). Under low irradiance conditions, insufficient ATP is produced for carbon fixation and carbohydrate biosynthesis, thus causing a decrease in P_N.

Plants under medium irradiance showed a significantly positive correlation between P_N and leaf length (Fig. 8*A*), suggesting that the increase of P_N promoted the growth of leaves. However, the correlation between P_N and leaf length was significantly negative under low irradiance (Fig. 8*A*), suggesting that the decrease in P_N promoted the increase in leaf length. The significant decrease of P_N under low irradiance caused by light deficiency would induce plants to increase organic matter accumulation by increasing leaf area, which is an adaption mechanism to low irradiance. It has been reported that the leaf area of shade-tolerant species increased with increasing shading degrees (Lusk 2002, Tang *et al.* 2022).

Shade can reduce transpiration because of the decrease in light intensity and leaf temperature induced by shade

(Ahemd *et al.* 2016, Lopez *et al.* 2018). In this study, the transpiration rate (*E*) of *A. gigantifolia* significantly decreased with the increase of shading (Fig. 3), indicating that the transpiration is restricted by shading, which is similar to *A. roxburghii* (Shao *et al.* 2014). In contrast, high irradiance induced the rise of leaf temperature and excessive transpiration, which resulted in a decrease in net photosynthetic rate (Liu *et al.* 2019, Yang *et al.* 2019). In *A. gigantifolia*, the significantly higher transpiration rate under high irradiance would be partially responsible for the significantly lower P_N under high irradiance (Figs. 3, 4).

The responses of Chl fluorescence to different light intensities: Measurement of Chl fluorescence is commonly used for the investigation of photosynthetic regulation and plant responses to the environment (Schreiber *et al.* 1995). Plants under medium irradiance presented a markedly higher value of F_v/F_m, F_v/F_0, and ETR than those under high irradiance, suggesting that moderate shading contributes to improving the utilization rate of light energy and alleviate the photoinhibition caused by excessive irradiance (Fig. 5*A–C*). However, low irradiance resulted in a significant decrease of F_v/F_m, F_v/F_0, and ETR compared to medium irradiance, revealing that severe shading would result in the decrease of PSII center activity and make *A. gigantifolia* suffer from low light stress (Fig. 5*A–C*). Under high and low irradiance conditions, the significantly lower value of F_v/F_m, F_v/F_0, and ETR would be partially responsible for the significantly lower photosynthetic rate (Figs. 4, 5*A–C*). However, the correlation between P_N and F_v/F_m, ETR, and q_P was not significant under the three shade treatments (Fig. 8*B*), suggesting that photosynthetic rate would not only be determined by a single Chl fluorescence parameter. Besides, the photosynthetic rate is also affected by many other factors, such as light intensity, transpiration, and oxidative stress (Liu *et al.* 2019, Yang *et al.* 2019, Xu *et al.* 2020).

Plants have evolved varieties of photoprotection strategies to adapt to high irradiance conditions, such as NPQ (Ruban *et al.* 2012). Plants can dissipate redundant light energy as heat energy harmlessly when suffering excessive irradiance to reduce the damage to apparatus caused by photoinhibition (Müller *et al.* 2001, Baker 2008). The larger NPQ represents the greater ability of plants to convert excess light energy into heat dissipation (Müller *et al.* 2001). In this study, plants under high irradiance exhibited the highest NPQ and the lowest q_P, demonstrating that *A. gigantifolia* adapted to a strong light environment by dissipating heat under high irradiance conditions (Fig. 5*D*,*E*).

The value of NPQ increased with the increase of light intensities and plants suffering photoinhibition usually exhibited a significantly higher value of NPQ (Shao *et al.* 2014, Yu *et al.* 2022). Plants under high irradiance showed a significantly negative correlation between P_N and NPQ, while the correlations were insignificant in plants under medium and low irradiance (Fig. 8*B*). These results indicated that the high NPQ caused by photoinhibition under high irradiance restricted photosynthetic rate of *A. gigantifolia*, while this restriction was alleviated and insignificant under medium and low irradiance.

The responses of Chl content to different light intensities: Chls are the major light-absorbing pigments of terrestrial plants. The content and proportion of Chls are important indexes reflecting the adaption of plants to different environments. Shade-tolerant plants generally had higher Chl (*a*+*b*) content under low irradiance compared to high irradiance (Shao *et al.* 2014, Yang *et al.* 2019). In this study, the contents of Chl *a*, Chl *b*, and Chl (*a*+*b*) increased significantly with the increase of shading (Fig. 6). The higher content of Chls can help *A. gigantifolia* capture light energy to survive under shade. Chl *a* and Chl *b* have different absorption spectra. Chl *a* has a stronger ability to absorb red light (longer light wavelengths), while Chl *b* has a stronger ability to absorb blue and purple light (shorter light wavelengths). Shade leads to the proportion of blue and purple light increase. The decrease in the Chl *a*/*b* ratio can improve the utilization efficiency of blue and purple light. In this study, the Chl *a*/*b* ratio under low irradiance was significantly lower than those under high and medium irradiance (Fig. 6). The decrease of Chl *a*/*b* under low irradiance conditions facilitated *A. gigantifolia* improve the light harvesting and utilizing the capacity of chlorophylls, which is an adaption mechanism to severe shading.

The responses of MDA content and POD activity to different light intensities: Abiotic stress induces plants to produce large amounts of reactive oxygen species (ROS). The increase in ROS leads to the production of MDA and damage to the cellular membrane. The MDA content reflects the degree of damage and stress in plants (Shah *et al.* 2001, Sharma and Dubey 2007). Plants under high irradiance exhibited significantly higher MDA content than plants under medium and low irradiance (Fig. 7). This suggested that shade effectively reduced the production of MDA, thus reducing the damage caused by excessive irradiance. The MDA content decreased first and then increased with the increasing shading (Fig. 7), which is similar to the results in *Poa pratensis* and *Festuca rubra* (De *et al.* 2015). This suggested that both excessive irradiance and severe shading resulted in plants suffering stress (Fig. 7). Besides, the significantly higher MDA content under high irradiance than low irradiance indicated that *A. gigantifolia* suffered higher stress under high irradiance compared to low irradiance (Fig. 7). Plants under high and low irradiance exhibited significant negative correlations between F_v/F_m and MDA, while there was no significant correlation under medium irradiance (Fig. 8*D*). This suggested that the high oxidative stress under high and low irradiance significantly inhibited the photosynthetic activity of *A. gigantifolia*, while this inhibition was insignificant under medium irradiance.

PODs are important protective enzymes in the anti-oxidant enzyme system and function as the major scavenger of H_2O_2 (Shah *et al.* 2001). Plants under high

irradiance presented the highest POD activity that was significantly higher than those under medium and low irradiance, which is beneficial to alleviate the damage caused by oxidative stress (Fig. 7). This suggested that *A. gigantifolia* enhanced the activity of POD enzymes to alleviate the damage caused by ROS under high irradiance, thus adapting to high irradiance. This is similar to the results in *Eremochloa ophiuroides* (Zhou and Cao 2006). The activity of the antioxidant enzyme maintains low in the case of low production of ROS (Zhou and Cao 2006). The significantly lower POD activity of *A. gigantifolia* under medium and low irradiance may be attributed to the significantly lower MDA content under medium and low irradiance compared to high irradiance.

Conclusion: In this study, *A. gigantifolia* had the best performance in growth, photosynthesis, and light-utilization efficiency under medium irradiance. Plants under high irradiance and low irradiance suffered from photoinhibition and light deficiency, respectively. Therefore, medium irradiance was the optimum light condition for the growth of *A. gigantifolia* in this study. *A. gigantifolia* can adapt to excessive irradiance and severe shading conditions by adjusting a series of physiological parameters, suggesting that *A. gigantifolia* has strong physiological plasticity.

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