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ARTICLE

Comparative Physiological Responses of Two *Bougainvillea* Cultivars to Shade Conditions

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ABSTRACT: The growth and landscape application of *Bougainvillea*, a widely cultivated ornamental plant, are often influenced by light conditions. The effects of shade on two *Bougainvillea* cultivars, 'Imperial Delight (ID)' and 'San Diego Red (SDR)', cultivated under full sunlight (CK) and 50% shade (S) were investigated. Under shading, both cultivars presented decreased leaf thickness; increased chlorophyll a, b and total contents; and reduced light compensation points (LCPs) and dark respiration rates (R_ds), reflecting morphological and photosynthetic acclimatization. Decreased superoxide dismutase (SOD) activity and malondialdehyde (MDA) contents indicated attenuated membrane lipid peroxidation. In 'ID', shading significantly reduced the leaf, bract and branch dimensions, and decreased the soluble sugar and protein contents, and the apparent quantum efficiency (AQY), reflecting reduced growth potential. In contrast, 'SDR' exhibited significant increases in leaf and bract dimensions and branch length under shade, with relatively small reductions in the soluble protein content and AQY, indicating less growth suppression. Integrated multivariate and correlation analyses revealed overall differences in physiological responses to shading, identifying seven representative indicators related mainly to the leaf phenotype and chlorophyll content. In summary, coordinated physiological and metabolic regulation may underlie the cultivar-specific differences. Both cultivars exhibited a certain adaptability to shading, but 'SDR' performed better than 'ID', suggesting a possible advantage under shade. This study provides a valuable theoretical foundation for the shade-tolerant cultivation and breeding of *Bougainvillea* germplasms.

KEYWORDS: *Bougainvillea*; shading; photosynthetic characteristics; morphological traits; physiological response

1 Introduction

Light is among the critical environmental factors influencing plant growth and development [1]. As light is the sole energy source for photosynthesis, biomass accumulation, and morphogenesis in plants, alterations in light intensity and spectral composition profoundly affect plant growth, physiological metabolism, and the synthesis of secondary metabolites [2]. Due to the high building density and increasing demands for vertical greening, shading has become a widespread and crucial environmental factor affecting plant growth in urban landscape ecosystems [3]. Studies have shown that shaded environments lead to reduced light intensity and altered spectral quality, triggering a series of adaptive responses in plants [4]. These include morphological changes such as increased plant height, elongated internodes, and expanded leaf area, as well as physiological adjustments in leaf photosynthetic pigment content, photosynthetic rate, and antioxidant enzyme activities [5]. However, excessive shading can result in insufficient photosynthetically

active radiation, leading to reduced accumulation of assimilates [6]. This subsequently causes a range of issues in landscape plants, including weakened vegetative growth and delayed or reduced flowering, thereby significantly compromising their reproductive growth [7].

During long-term evolution, plants have developed a series of complex shade tolerance adaptation strategies in response to low-light conditions, which can be broadly categorized into shade avoidance strategies and shade tolerance strategies [5]. Shade avoidance manifests primarily morphologically, for instance, by promoting the elongation of hypocotyls and internodes, increasing plant height, and altering individual leaf area, thereby maximizing the capture of limited light resources [8]. In contrast, the shade tolerance strategy involves adaptive adjustments mainly at the physiological and biochemical levels [9]. In terms of the photosynthetic system, plants increase the chlorophyll content in leaves and reduce the chlorophyll a/b ratio, thereby improving the capture efficiency of light-harvesting pigment protein complexes for diffuse light and blue–violet light [9]. Concurrently, adjustments occur in the photosynthetic apparatus, such as increasing the maximum photochemical efficiency and the actual photochemical efficiency of photosystem II (PSII) while lowering the LCP and R_d, thus optimizing energy use efficiency under low-light conditions [10]. Furthermore, in terms of carbon metabolism, plants may allocate a greater proportion of assimilates to leaf growth than to root or reproductive structures, reflecting a trade-off strategy under resource-limited conditions [11]. The plant antioxidant defense system also undergoes rapid changes in response to shade, alleviating reactive oxygen species-induced damage and maintaining cell membrane stability [12]. These multilevel, interconnected adaptive responses collectively form the foundation of plant shade tolerance, although their specific manifestations and extents exhibit significant intraspecific and interspecific variation [13].

Bougainvillea spp., evergreen woody vines belonging to the Nyctaginaceae family, are important ornamental plants in tropical and subtropical regions worldwide [14]. Valued for their vibrant bracts, prolonged flowering period, and strong environmental adaptability, they are widely used in urban landscaping, vertical greening, and bonsai art [15]. Their ornamental value is derived primarily from their specialized bracts, making the bract area a key indicator of visual quality [16]. Although *Bougainvillea* is generally considered a light-demanding species, with sufficient light being a prerequisite for normal growth and development, many cultivars are inevitably subjected to varying degrees of shade in practical horticultural settings [17]. To date, research on the effects of light on *Bougainvillea* has focused predominantly on cultivation under full-sun conditions. Considerable variation exists among different *Bougainvillea* cultivars in terms of genetic background, morphological traits, and physioecological adaptability, which may lead to divergent response strategies and tolerance capacities under shade conditions [18]. This variability among germplasm resources provides a theoretical basis for selecting and breeding new shade-tolerant cultivars and for facilitating their scientific application in specific low-light environments. However, systematic comparative studies on the integrated response mechanisms of different *Bougainvillea* cultivars to shaded conditions, encompassing growth morphology, photosynthetic characteristics and antioxidant defense systems, remain insufficient.

Therefore, this study aims to systematically assess the response patterns of growth performance and key physiological characteristics, including photosynthetic parameters, soluble sugar and soluble protein contents, and antioxidant enzyme activities, in representative *Bougainvillea* cultivars under shading treatment. This research is expected to elucidate the adaptation strategies of different *Bougainvillea* cultivars to low-light environments and reveal the physiological mechanisms underlying their shade tolerance. These findings provide a scientific basis and practical guidance for *Bougainvillea* cultivar selection, cultivation management, and landscape design in composite light horticultural habitats.

2 Materials and Methods

2.1 Experimental Materials

The test materials consisted of two commercially popular *Bougainvillea* cultivars, *Bougainvillea* × *spectoglabra* 'ID' and *Bougainvillea* × *buttiana* 'SDR', were sourced from Zhangzhou, Fujian. Healthy three-year-old seedlings with uniform heights and well-developed root systems were selected for the experiment and planted in uniformly sized plastic pots. The pots had top diameters, bottom diameters, and heights of 21.5 cm, 18 cm, and 15 cm, respectively, and were filled with a substrate consisting of garden soil, perlite, and vermiculite at a 2:1:1 ratio. The experiment was conducted in a nursery located at Minnan Normal University (24°30′ N, 117°38′ E). During July and August, the average temperature in the nursery was 34.25°C, and the average relative humidity was 75.42%. Zhangzhou features a southern subtropical maritime monsoon climate characterized by flat terrain and low water tables. The region has an annual average temperature of 23°C, approximately 2035 h of sunshine, and 1400 mm of average rainfall.

2.2 Shading Treatment

In May 2023, the two *Bougainvillea* cultivars were placed in the experimental nursery and subjected to routine field management. Shading treatments commenced in July 2023. For each cultivar, the plants were randomly divided into two groups: full sunlight (control) and 50% shade (achieved by using a black shade net). The average photosynthetically active radiation (PAR) was 1700 μmol·m^{-2}·s^{-1} under full light and 850 μmol·m^{-2}·s^{-1} under 50% shading. All the pots were randomly arranged before the experiment and placed inside the test area away from the edges to avoid edge effects. Each individual potted *Bougainvillea* seedling was defined as one independent biological replicate, with three replicates per treatment. Three samples per plant were measured as technical replicates, and the average value was recorded. All the plants received consistent fertilization and watering regimens. Measurements were conducted after 60 days of shading treatment.

2.3 Measurement of Morphological Indicators

Before the shading treatments were initiated, branches of similar length and diameter from healthy plants were selected and labeled with colored tape, and their lengths were measured. Fully expanded, disease-free functional leaves from the upper section of each plant were selected for trait measurements. The length and width of the leaves and bracts were measured using Vernier calipers. Leaf area was measured using the application Leaf-IT, which calculates the area based on digital image processing technology [19]. Leaf thickness was measured at the midpoint of the leaf blade, avoiding the midrib, with the same Vernier caliper. All measurements were performed using uniform operational criteria; each sample was measured three times, and the mean value was calculated to guarantee the reliability of the data.

2.4 Measurement of the Chlorophyll Content and Photosynthetic Indicators

After 60 days of shading treatment, functional leaves from the same nodal position were collected for physiological measurements. The chlorophyll content was quantified according to the method described by Arnon [20]. The chlorophyll content was measured using an ultraviolet spectrophotometer (Shimadzu UV-1750, Japan). Fresh leaf samples were extracted with 80% (v/v) acetone. The homogenate was subsequently centrifuged at 5000× *g* for 10 min, after which the absorbance of the supernatant was recorded

at 663 nm and 645 nm. The chlorophyll concentrations (mg·g^{-1} fresh weight) were calculated using the following equations:

Chlorophyll a (Chl a) = 12.7(A_{663}) − 2.69(A_{645})

Chlorophyll b (Chl b) = 22.9(A_{645}) − 4.68(A_{663})

Chlorophyll a/b = Chl a/Chl b

Total chlorophyll = Chl a + Chl b

Photosynthetic characteristics were measured with a portable photosynthesis system (LI-6400, Li-COR, Lincoln, NE, USA) following the method described in a previous study [21]. The light intensity gradient was set at 2000, 1600, 1200, 800, 400, 200, 100, 50, 25, and 0 μmol·m^{-2}·s^{-1}. The photosynthetic light response curve was fitted using a modified rectangular hyperbola model [22]. The relevant characteristic parameters, including the LCP, light saturation point (LSP), AQY and R_d, were calculated accordingly. The fitting formulas are as follows:

$$P_n = \alpha \frac{1-\beta I}{1+\gamma I} I - R_d$$

$$LCP = \frac{\alpha - \gamma R_d - \sqrt{(\gamma R_d - \alpha)^2 - 4\alpha\beta R_d}}{2\alpha\beta}$$

$$LSP = \frac{\sqrt{(\beta+\gamma)/\beta} - 1}{\gamma}$$

where I is the photosynthetic photon flux density, and α is the AQY value, and β and γ are coefficients that are independent of I. The R_d value is the absolute value of P_n measured when I = 0.

2.5 Measurement of Physiological Indicators

SOD activity was determined using the nitro blue tetrazolium (NBT) reduction assay [23]. The MDA content was measured via the thiobarbituric acid (TBA) method [24]. Soluble sugar levels were analyzed by the anthrone-sulfuric acid method [25], and the soluble protein content was estimated using the Coomassie brilliant blue G-250 binding assay [26].

2.6 Multivariate Analysis and Data Processing

The data were analyzed using Excel 2019. The significance levels of the effects of the cultivar, shading treatment, and their interactions were determined using two-way ANOVA in IBM SPSS Statistics 27.0. Hierarchical clustering and OPLS-DA were conducted using the MetaboAnalyst 6.0 platform. The robustness of the model was determined using a permutation test (n = 1000). The variable importance in projection (VIP) values from the OPLS-DA were used to assess the relative contribution of each indicator to shading discrimination, with those exceeding 1.0 considered key indicators. Correlation analysis of physiological indicators was conducted using Origin 2025b.

3 Results

3.1 Alterations in the Morphology of Bougainvillea Following Shading Treatment

Shading treatment significantly influenced the leaf morphological parameters of the two *Bougainvillea* cultivars (Fig. 1). Significant cultivar × shading interactions were observed for the leaf length, width and area (Fig. 1A–C), indicating divergent responses between the two cultivars. The leaf thickness showed only a significant main effect of shading (Fig. 1D), whereas no significant effects were observed for the branch length (Fig. 1E). In 'ID', the leaf length, width, and area under 50% shade were significantly lower than those under full sunlight, with decreases of 15.85% ($p < 0.05$), 36.01% ($p < 0.001$), and 56.52% ($p < 0.001$), respectively (Fig. 1A–C). Conversely, in 'SDR' under identical shading conditions, the leaf length, width, and area exceeded those under full sunlight (Fig. 1A–C). Specifically, the leaf length and area significantly increased, with increases of 19.33% ($p < 0.05$) and 16.15% ($p < 0.001$), respectively, whereas the leaf width slightly increased by 3.20% (Fig. 1A–C). Compared with that under full sunlight, the leaf thickness under shade decreased for both cultivars (Fig. 1D). Additionally, shading treatment altered the branch length of the two *Bougainvillea* cultivars. Compared with the full sunlight control, 'ID' resulted in a 15.47% reduction, whereas 'SDR' resulted in a 24.17% increase (Fig. 1E).

Significant main effects of cultivar and cultivar × shading interactions were also observed for the bract length and bract width (Fig. 1F,G). Under 50% shade, the length and width of the 'ID' bracts were significantly reduced by 8.80% ($p < 0.05$) and 22.78% ($p < 0.001$), respectively, compared with those in the full-sunlight control (Fig. 1F,G). Conversely, 'SDR' exhibited highly significant increases in bract length and width ($p < 0.001$), with increases of 52.89% and 33.33%, respectively, under shading conditions (Fig. 1F,G).

3.2 Alterations in Chlorophyll Accumulation in Bougainvillea Following Shading Treatment

To investigate the effects of shading treatment on chlorophyll accumulation in *Bougainvillea* leaves, we measured the chlorophyll contents in the leaves of the two cultivars. The results demonstrated that significant cultivar × shading interactions were observed for the chlorophyll a and total chlorophyll (Fig. 2A,C). The chlorophyll b showed significant main effects of cultivar and shading (Fig. 2B), whereas for the chlorophyll a/b ratio, only the shading effect was significant (Fig. 2D). Under 50% shade conditions, the chlorophyll a (Chl a), chlorophyll b (Chl b), and total chlorophyll contents significantly increased in both cultivars compared with those in the full-sunlight controls (Fig. 2A–C). In 'SDR', the Chl a, Chl b, and total chlorophyll contents significantly increased ($p < 0.001$), with increases of 61.17%, 120.36%, and 76.13%, respectively (Fig. 2A–C). The 'ID' resulted in highly significant increases in the Chl a and total chlorophyll contents ($p < 0.001$), which increased by 19.53% and 30.64%, respectively (Fig. 2A,C), while the Chl b content increased significantly by 62.74% ($p < 0.01$) (Fig. 2B). Moreover, shading treatment significantly altered the Chl a/b ratio (Fig. 2D). Both cultivars displayed lower Chl a/b ratios under 50% shade than under full light (Fig. 2D). Specifically, 'SDR' exhibited a reduced Chl a/b ratio of 2.16, representing a significant 27.92% decrease ($p < 0.05$) (Fig. 2D). 'ID' had a Chl a/b ratio of 2.20, corresponding to a significant 24.14% reduction ($p < 0.05$) (Fig. 2D). Collectively, these findings indicate that shading promotes chlorophyll accumulation in *Bougainvillea* leaves, with a proportionally greater increase in Chl b, thereby reducing the Chl a/b ratio. This adaptive response may improve the light-harvesting capacity under low-light conditions, which could be beneficial for light utilization.

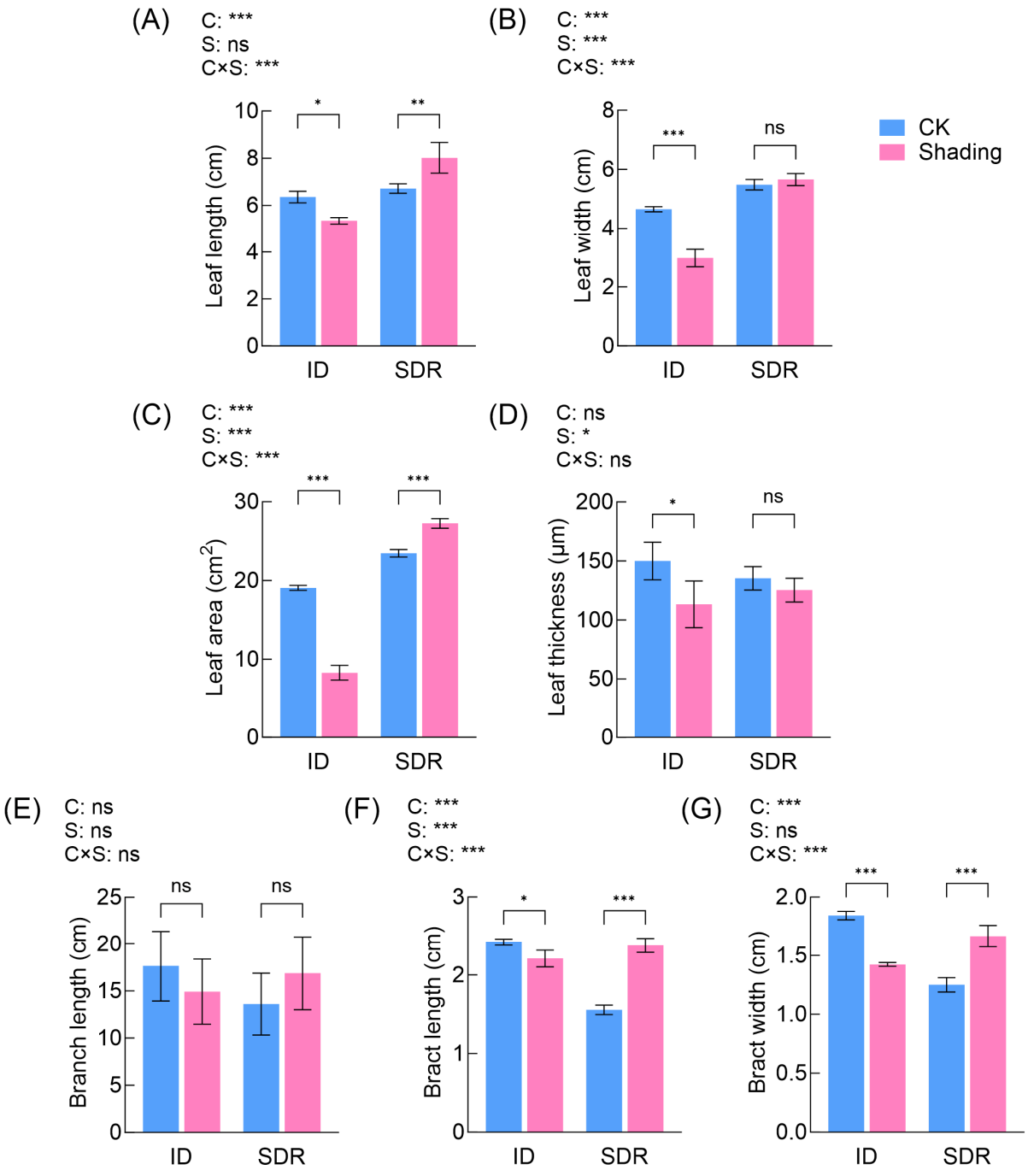

Figure 1: Effects of shading treatment on the morphological indices of two *Bougainvillea* cultivars. (**A**) Leaf length. (**B**) Leaf width. (**C**) Leaf area. (**D**) Leaf thickness. (**E**) Branch length. (**F**) Bract length. (**G**) Bract width. The values are expressed as the mean ± standard error (SE; n = 3). The error bars represent SEs. C, cultivar effect; S, shading effect; C×S, cultivar × shading interaction effect from two-way ANOVA. Significant differences are denoted by asterisks (*p < 0.05, **p < 0.01 and ***p < 0.001). ns, no significant difference.

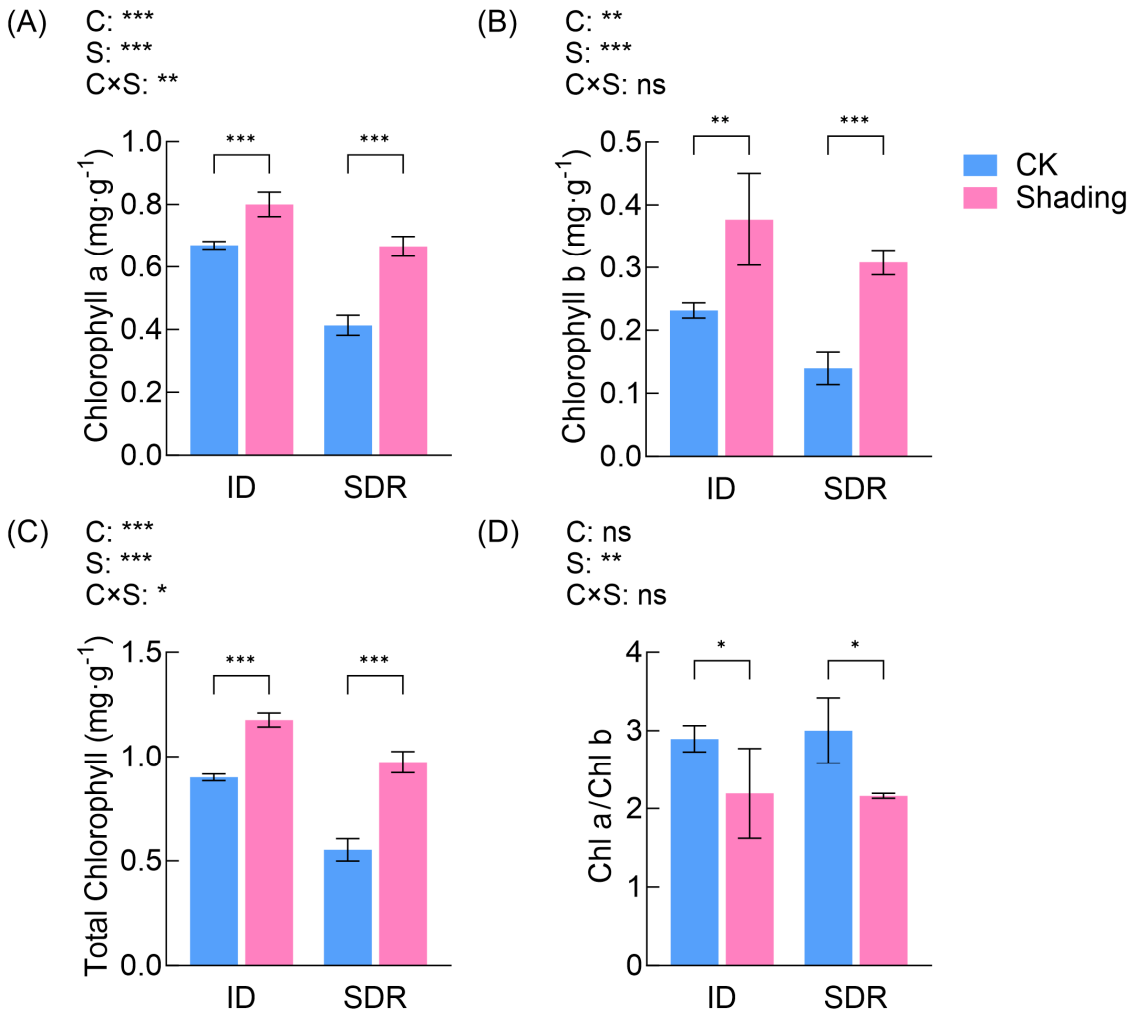

Figure 2: Effects of shading treatment on the chlorophyll content of two *Bougainvillea* cultivars. (**A**) Chlorophyll a content. (**B**) Chlorophyll b content. (**C**) Total chlorophyll content. (**D**) Chl a/Chl b. The values are expressed as the mean ± standard error (SE; n = 3). The error bars represent SEs. C, cultivar effect; S, shading effect; C×S, cultivar × shading interaction effect from two-way ANOVA. Significant differences are denoted by asterisks (*p < 0.05, **p < 0.01 and ***p < 0.001). ns, no significant difference.

3.3 Alterations in Bougainvillea Photosynthesis Following Shading Treatment

To further analyze the effects of shading treatment on photosynthesis in *Bougainvillea*, we measured the leaf LCP, LSP, R_d, and AQY (Fig. 3). The results demonstrated a significant main effect of shading and a significant cultivar × shading interaction for LCP (Fig. 3A). R_d showed significant main effects of cultivar and shading (Fig. 3C), whereas neither the main effects nor the interaction effects were statistically significant for LSP and AQY (Fig. 3B,D). Under 50% shade, the LCPs of both 'ID' and 'SDR' were lower than those under full sunlight, with 'ID' decreasing slightly by 3.05% and 'SDR' decreasing more significantly by 42.67% (p < 0.01) (Fig. 3A). The LSP value of 'ID' increased by 11.29%, whereas that of 'SDR' only slightly increased by 0.88% (Fig. 3B). Shading treatment reduced the R_d and AQY of *Bougainvillea*; in terms of R_d, 'ID' decreased by 30.56% (p < 0.05), and 'SDR' decreased by 42.71% (p < 0.05) (Fig. 3C), whereas the AQY of 'ID' decreased by 28.38%, and that of 'SDR' slightly decreased by 2.11% (Fig. 3D).

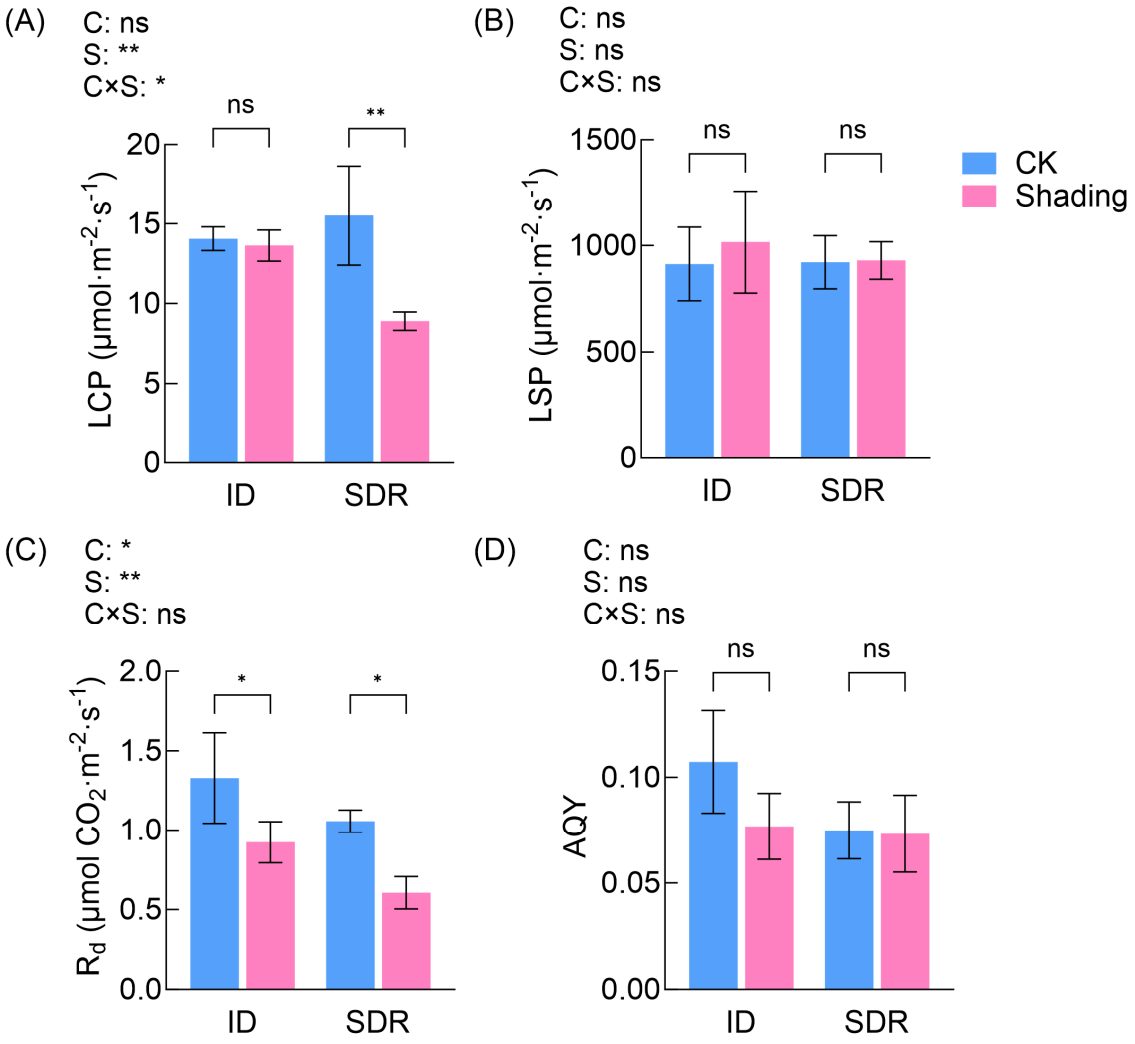

Figure 3: Effects of shading treatment on the photosynthesis indices of two *Bougainvillea* cultivars. (**A**) LCP. (**B**) LSP. (**C**) R_d. (**D**) AQY. The values are expressed as the mean ± standard error (SE; n = 3). The error bars represent SEs. C, cultivar effect; S, shading effect; C×S, cultivar × shading interaction effect from two-way ANOVA. Significant differences are denoted by asterisks (*p < 0.05 and **p < 0.01). ns, no significant difference.

3.4 Alterations in Key Physiological Parameters of Bougainvillea Following Shading Treatment

To further investigate the physiological responses of *Bougainvillea* leaves to shading treatment, key indicators of oxidative stress and osmotic adjustment, including MDA content, SOD activity, and soluble sugar, and soluble protein contents, were measured. The results revealed significant cultivar × shading interactions for SOD activity and soluble protein content (Fig. 4B,D), whereas MDA and soluble sugar content exhibited only significant main effects of cultivar and shading, with non-significant interactions (Fig. 4A,C). Under 50% shade, compared with full sunlight, 'ID' resulted in a significant 29.22% reduction in the MDA content (p < 0.05), whereas 'SDR' resulted in a 28.97% decrease (Fig. 4A). Following shading treatment, SOD activity decreased in both cultivars (Fig. 4B). Compared with that of the control, the SOD activities of 'ID' and 'SDR' decreased slightly by 2.23% and 8.94% (p < 0.001), respectively. (Fig. 4B). Both the soluble sugar and soluble protein contents decreased under shading (Fig. 4C,D). The soluble sugar contents in 'ID' and 'SDR' significantly decreased by 21.37% (p < 0.001) and 29.10% (p < 0.001), respectively (Fig. 4C).

Additionally, the soluble protein content in 'ID' decreased significantly by 85.20% ($p < 0.001$), whereas that in 'SDR' slightly decreased by 5.24% (Fig. 4D).

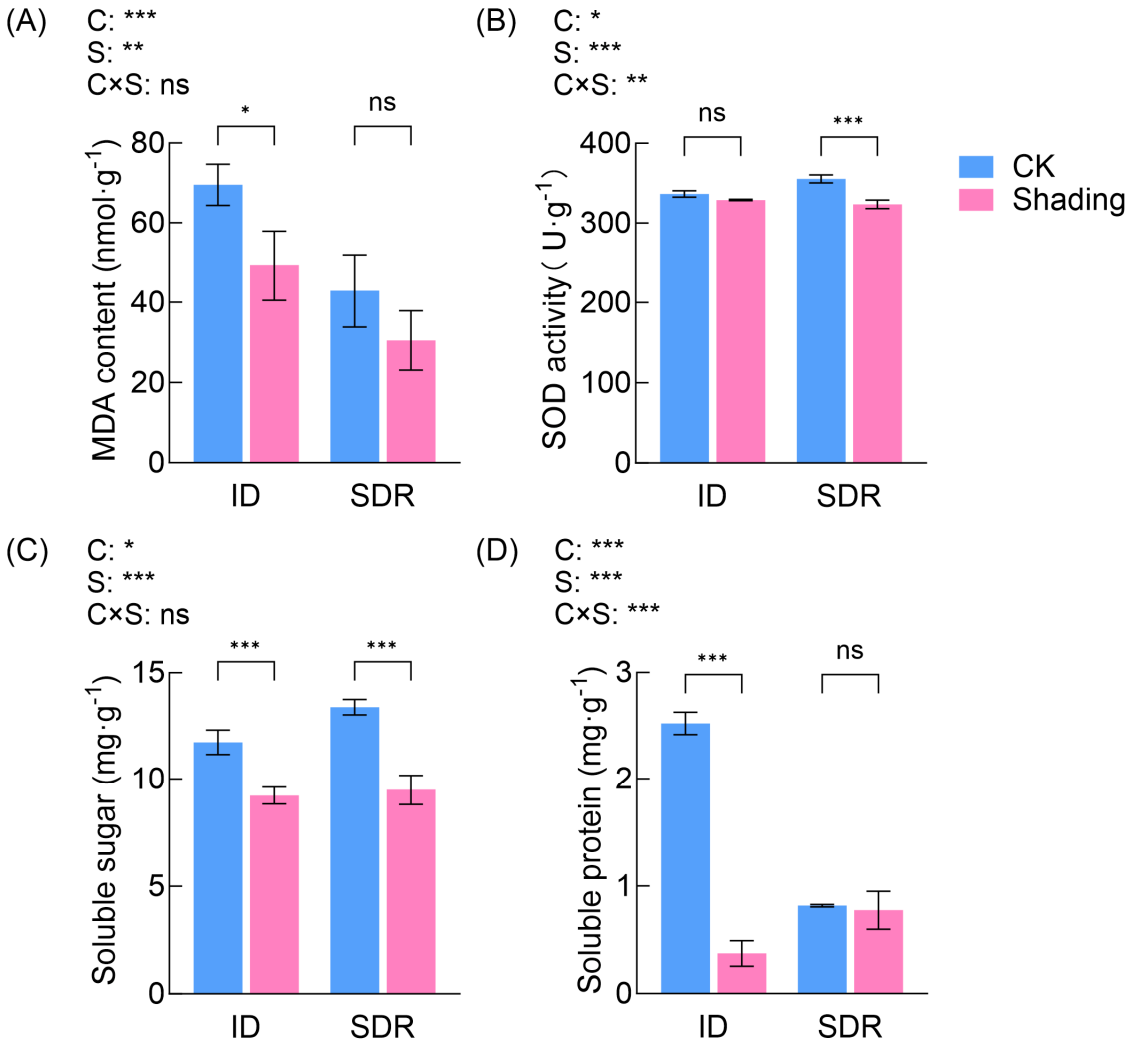

Figure 4: Effects of shading treatment on the oxidative stress and osmotic adjustment indices of two *Bougainvillea* cultivars. (**A**) MDA content. (**B**) SOD activity. (**C**) Soluble sugar content. (**D**) Soluble protein content. The values are expressed as the mean ± standard error (SE; n = 3). The error bars represent SEs. C, cultivar effect; S, shading effect; C×S, cultivar × shading interaction effect from two-way ANOVA. Significant differences are denoted by asterisks (*$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$). ns, no significant difference.

3.5 Integrated Multivariate Analysis of the Differences in the Physiological Responses of Bougainvillea Following Shading Treatment

To characterize the overall differences in physiological responses between the two *Bougainvillea* cultivars, an integrated multivariate analysis combining hierarchical clustering and OPLS-DA was conducted (Fig. 5). Construction of a hierarchical clustering heatmap based on 19 physiological indices revealed two distinct major clusters corresponding to the control and shading treatments. Within each treatment cluster, all the ID and SDR samples were clustered into distinct groups separately, indicating inherent physiological divergence between the two cultivars (Fig. 5A).

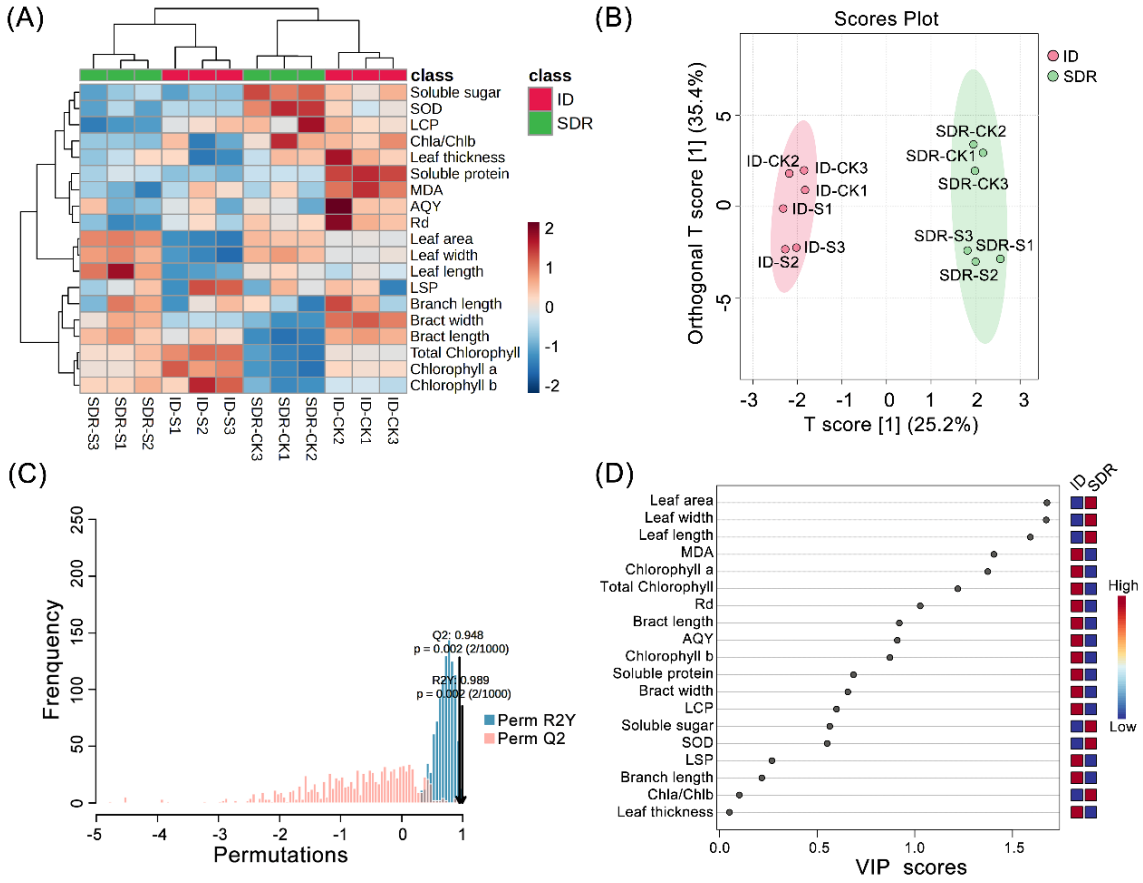

Figure 5: Integrated multivariate analysis of physiological differences between two *Bougainvillea* cultivars. (**A**) Hierarchical clustering heatmap of 19 physiological indices. CK: control; S: shading. (**B**) OPLS-DA score plot. (**C**) Permutation test plot (n = 1000) confirming the robustness of the OPLS-DA model. (**D**) VIP plot of the predictive component.

A supervised OPLS-DA model was further applied to quantify the differences in physiological responses observed between the two cultivars (Fig. 5B). The OPLS-DA scores plot projected samples onto the predictive component (T score) and the first orthogonal component (orthogonal T score), which accounted for 25.2% and 35.4% of the total variance, respectively (Fig. 5B). The predictive component showed apparent separation between the samples of the two cultivars (ID vs. SDR), whereas the orthogonal component primarily reflected shading effects (CK vs. S) (Fig. 5B). This trend was consistent with the results of the hierarchical clustering analysis shown in the heatmap (Fig. 5A).

To confirm the statistical robustness of the OPLS-DA model, a permutation test (n = 1000) was performed (Fig. 5C). The R^2Y and Q^2 values of the original model were 0.989 and 0.948, respectively, which were substantially greater than those of all the permuted models (p = 0.002) (Fig. 5C). These results demonstrated the reliability of the OPLS-DA model. Variable importance in projection (VIP) analysis of the predictive component revealed key physiological indices driving cultivar discrimination (Fig. 5D). VIP values > 1 were considered major contributors to the observed physiological differences, including leaf area (1.68), leaf width (1.67), leaf length (1.59), MDA (1.40), chlorophyll a (1.37), total chlorophyll (1.21) and R_d (1.03) (Fig. 5D). These potentially screened physiological indicators may play a certain role in distinguishing the differential

responses of the two cultivars to shading. However, the grouping may also reflect inherent genotypic differences between the two cultivars rather than the effects of shading alone.

3.6 Correlations of the Physiological Parameters of Bougainvillea Following Shading Treatment

To examine the relationships among the different physiological parameters, pairwise Pearson correlation analysis was performed on the 19 measured physiological indicators (Fig. 6). The correlation coefficient matrix revealed 43 significant correlations ($p < 0.05$), including 26 significantly positive and 17 significantly negative correlations (Fig. 6). For instance, leaf length, leaf width, and leaf area were significantly positively correlated with each other. Similarly, R_d, AQY, and MDA were significantly positively correlated (Fig. 6). Furthermore, bract length was significantly positively correlated with chlorophyll a, chlorophyll b, and total chlorophyll content. In contrast, leaf width was significantly negatively correlated with chlorophyll a, chlorophyll b, and total chlorophyll content (Fig. 6). SOD activity and soluble sugar content showed similar correlation patterns: both were significantly negatively correlated with bract length and chlorophyll a, chlorophyll b, and total chlorophyll content but significantly positively correlated with the Chl a/Chl b ratio and LCP (Fig. 6). Additionally, soluble protein was significantly positively correlated with leaf thickness, bract width, R_d, AQY and MDA (Fig. 6).

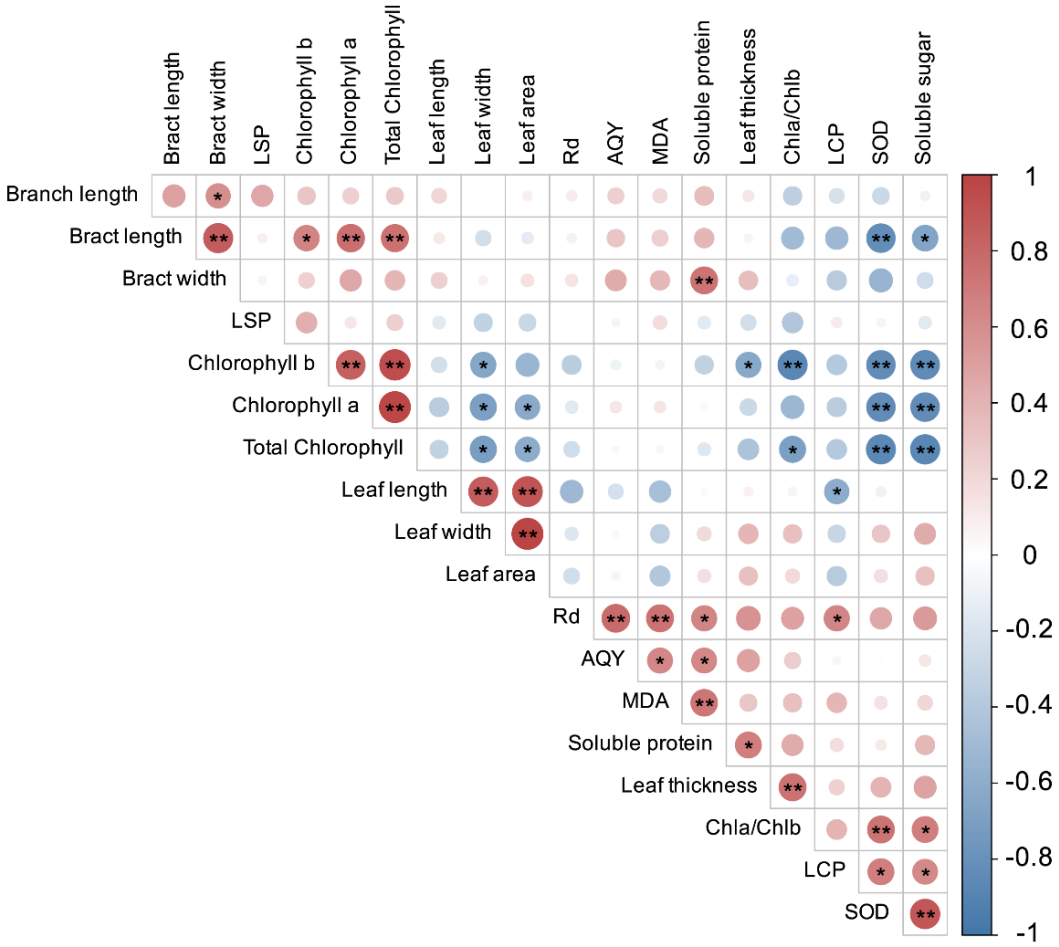

Figure 6: Correlation analysis between 19 indices of *Bougainvillea*. Significant differences are denoted by asterisks (*$p < 0.05$ and **$p < 0.01$).

4 Discussion

4.1 Effects of Shading Treatment on the Phenotypic Traits of Bougainvillea

Light is an indispensable environmental factor for plant survival and growth [27]. Different light intensities can lead to significant phenotypic differences in plants, and these phenotypic changes reflect the adaptation strategies of plants to their light environment [28]. Previous studies have shown that under low-light conditions, plants allocate more biomass to their leaves by increasing the total leaf area and directing more nutrients toward the development of supportive structures and conductive tissues, thereby increasing light capture efficiency and improving their shade tolerance [29]. In this study, compared with those of the respective controls, the leaf length, width, and area of 'SDR' tended to increase after shading treatment, whereas the leaf length, width, and area of 'ID' significantly decreased compared with those of the respective controls (Fig. 1A–C). These findings indicate that the two cultivars respond differently to low-light conditions, which may be important manifestations of their differences in shade tolerance. Moreover, *Bougainvillea* leaf thickness decreased after shading (Fig. 1D), suggesting that leaf thinning may facilitate the penetration of radiation through the leaf epidermis to the mesophyll tissue, thereby increasing light capture and improving the efficiency of light energy conversion [30].

The change in branch growth induced by shading represents an important adaptive strategy of plants to low-light environments [31]. For example, in *Pinus yunnanensis* seedlings, moderate shading (50% shade) significantly promoted branch elongation, whereas severe shading (75% shade) suppressed branch growth [32]. In this study, after shading treatment, the branch length of 'ID' was shorter than that of the control, whereas that of 'SDR' was longer (Fig. 1E). It is speculated that under low-light conditions, 'SDR' exhibits stronger adaptability by promoting branch elongation, which contributes to competition for limited light resources to increase the ability to capture light energy. Shading treatment also has a significant effect on the development of plant floral organs [7]. For example, compared with the control treatment, shading treatment resulted in significant reductions in bract number and size in *Calathea crotalifera* [33]. In this study, the bract length and width of 'ID' significantly decreased after shading, whereas those of 'SDR' significantly increased (Fig. 1F,G). These findings suggest a possible advantage of 'SDR' in terms of bract size under shaded conditions. However, further research is still needed to screen more traits for a comprehensive assessment of the effects of shading on the ornamental value of *Bougainvillea*.

4.2 Effects of Shading Treatment on Photosynthesis in Bougainvillea

Under shaded conditions, plants often exhibit adaptive changes in chlorophyll content. Shade-tolerant plants typically present increased levels of chlorophyll a, chlorophyll b, and total chlorophyll and a decreased chlorophyll a/b ratio [34]. In shaded environments, leaves tend to accumulate more chlorophyll to increase light energy capture efficiency [35]. Among these pigments, chlorophyll b is more effective at utilizing scattered blue and violet light, and its increase in content under low-light conditions aids in improving light absorption, thereby promoting photosynthesis [36]. For example, in response to low-light stress, summer maize increased its content of chlorophyll b. This increased blue light absorption and capture, leading to improved light energy use efficiency, which serves as a key photoprotective adaptation to shading [37].

In this study, after shading treatment, both *Bougainvillea* cultivars presented significantly higher chlorophyll a, chlorophyll b, and total chlorophyll contents than their respective controls did (Fig. 2A–C), whereas the chlorophyll a/b ratio decreased significantly (Fig. 2D). The changes in the chlorophyll components and content of *Bougainvillea* are consistent with the typical pattern of low-light acclimation in plants, and we speculate that these results are attributed mainly to the active physiological acclimation of plants to

low-light conditions [38]. Previous studies have shown that leaf thinning under low-light conditions is caused primarily by the inhibition of cell division and expansion [39]. This morphological change is often accompanied by a reduced thickness of palisade tissue and decreased chloroplast numbers in leaves, which structurally constrain chlorophyll accumulation and remove the essential conditions for an increase in the chlorophyll concentration [40]. Therefore, although shading treatment led to a reduction in leaf thickness in both cultivars (Fig. 1D), we speculate that the observed increase in the chlorophyll content and decrease in the chlorophyll a/b ratio in this study were not concentration effects caused by leaf thinning but rather adaptive physiological acclimation traits formed by plants via the active regulation of chlorophyll synthesis and preferential accumulation of chlorophyll b to adapt to low-light environments.

Photosynthesis is a key indicator of plant growth capacity [41]. By altering their photosynthetic characteristics, plants adapt to varying light conditions, and these changes reflect their efficiency in utilizing light resources and their adaptability to low-light environments [42]. In this study, *Bougainvillea* subjected to shading treatment presented decreased LCPs (Fig. 3A). Studies have shown that plants with a lower LCP are typically adapted to shaded environments, as their photosynthetic systems can maintain net carbon accumulation under low-light conditions [43]. Moreover, the R_ds decreased, with the 'SDR' cultivar decreasing significantly after shading (Fig. 3C), suggesting that a reduced R_d may decrease the consumption of organic matter and energy [44]. In this study, the AQY of both *Bougainvillea* cultivars decreased after shading, but the decrease in the 'SDR' cultivar was minimal and not significantly different from that in the control (Fig. 3D), indicating that shading had little effect on light energy utilization efficiency, suggesting that the potential adaptability of 'SDR' to low-light environments is stronger than that of 'ID'. However, more comprehensive and complementary indicators, including the maximum net photosynthetic rate, intercellular CO_2 concentration, and chlorophyll fluorescence parameters, for assessing the differences in the photosynthetic capacity between the two cultivars after shading treatment still require further in-depth validation.

4.3 Effects of Shading Treatment on Oxidative Stress and Osmotic Regulation in Bougainvillea

Light profoundly influences physiological and metabolic processes through its intensity and quality in plants [2]. Under both natural and cultivated conditions, plants are frequently exposed to high-light stress, resulting in an overreduction of the electron transport chain in PSI and PSII and substantial accumulation of ROS, which subsequently induces oxidative damage [45]. Shading, as a common approach to modulating the light environment, can partially mitigate high light-induced oxidative stress by reducing light energy input [46]. For example, moderate shading treatment was optimal for the growth of *Melaleuca alternifolia* seedlings. Under these conditions, significant reductions in the leaf MDA content and SOD activity were observed [47]. The results of this study demonstrated that the MDA content slightly decreased in both cultivars following shading (Fig. 4A), suggesting that shading treatment alleviated membrane lipid peroxidation and effectively attenuated oxidative stress caused by light exposure. Furthermore, SOD activity decreased in both *Bougainvillea* cultivars after shading treatment, with a significant reduction observed in the 'SDR' cultivar (Fig. 4B), indicating a diminished requirement for increased antioxidant defense under the applied shading conditions. These results suggest that moderate shading conditions primarily relieve oxidative stress caused by high light exposure.

The reduction in light intensity caused by shading is a critical environmental factor for plants growing under canopies or in intercropping systems, profoundly influencing their carbon-nitrogen metabolic balance and resource allocation strategies [48]. The accumulation of soluble sugars, which are primary products of photosynthesis, is directly dependent on the supply of photoassimilates [49]. The results of this study

revealed that shading treatment significantly reduced the soluble sugar contents in the leaves of both *Bougainvillea* cultivars (Fig. 4C). It is hypothesized that the diminished light availability under shading conditions limited photosynthetic carbon fixation efficiency, thereby reducing the substrate supply required for the synthesis and accumulation of soluble sugars, ultimately leading to a decreased soluble sugar content in the leaves [50].

The soluble protein content is an important dynamic indicator of nitrogen metabolism and protein turnover [51]. Shading can reduce protein synthesis due to a limited energy supply for photosynthesis while promoting protein degradation to remobilize nitrogen in plants [52,53]. Under shading conditions, the soluble protein content also tended to decrease, with the reduction in the 'ID' cultivar being significantly more pronounced than that in the 'SDR' cultivar (Fig. 4D). The sharp decrease in the soluble protein content in 'ID' under shading may reflect more pronounced shade-induced proteolysis or the suppression of protein synthesis, which may be associated with its lower shade capacity than 'SDR'. In contrast, 'SDR' maintained relatively stable soluble protein levels under shading, suggesting a better ability to preserve protein homeostasis under low-light conditions. These findings indicate that the mechanisms underlying the response of soluble protein metabolism to shading differ between the two cultivars. The coordinated declines in both soluble sugar and soluble protein contents collectively reveal the tight coupling between carbon and nitrogen metabolism in *Bougainvillea* in shaded environments, as well as the dual limitations in carbon and nitrogen resources they face.

4.4 Integrated Analysis of Physiological Divergence and Indicator Correlations in Bougainvillea

Multivariate analytical strategies, including hierarchical clustering and OPLS-DA, have been widely employed to capture overall phenotypic differences in plant physiological studies [54,55]. In this study, the hierarchical clustering heatmap revealed differences in physiological responses between the two *Bougainvillea* cultivars (Fig. 5A). The distinct grouping observed in the OPLS-DA model further illustrated the physiological divergence between 'ID' and 'SDR' (Fig. 5B,C), which may be partially attributed to the inherent genotypic differences between the cultivars. Seven representative physiological indicators were screened based on the VIP value and were associated mainly with the leaf phenotype and chlorophyll content (Fig. 5D), suggesting that leaf development and photosynthetic performance may be closely linked to the response to shading in *Bougainvillea*. Similar results have been reported in other plants. For instance, the responses of two different *Opisthopappus* species, *O. taihangensis* and *O. longilobus*, to shading stress differ [56]. Key photosynthetic traits and chlorophyll contents both increase under shading, whereas morphological traits such as leaf thickness and stomatal aperture, along with antioxidant enzyme activities, tend to decrease [56]. These exploratory observations improve our understanding of the genotypic differences in shade responses, but the relevant conclusions still need further verification in expanded samples.

Correlation analysis among physiological indices provides insight into the coordinated regulation of plant metabolic networks [57]. In this study, the apparent correlations observed among multiple physiological indicators implied that the differential responses to shading between the two cultivars may have arisen from coordinated adjustments across multiple physiological pathways (Fig. 6). Close correlations among photosynthetic characteristics, antioxidant enzyme activities, and substances related to the osmotic adjustment were observed under shading conditions (Fig. 6), suggesting a potential synergistic physiological strategy for maintaining cellular homeostasis in *Bougainvillea*. Consistent with findings in other plants, seedlings of *Pterocarpus indicus* under shading treatment exhibit a significant reduction in leaf area and differential expression of photosynthesis-related genes, indicating physiological and morphological acclimation to low-light conditions [58]. *Quercus robur* adapts to shade through coordinated adjustments in

photosynthesis, increased synthesis of chlorophyll and carotenoids, activation of antioxidant defense, and osmotic regulation [59]. These results suggest that coordinated physiological and metabolic regulation may lead to the distinct overall physiological profiles of the two *Bougainvillea* cultivars under shading treatment. However, considering the limited sample size and potential bias arising from multiple comparisons, these correlations require further validation.

5 Conclusion

In conclusion, in this study, we comprehensively compared the physiological responses of two *Bougainvillea* cultivars under shading treatment. Both cultivars demonstrated a certain adaptability to shading, but significant intercultivar differences in physiological performance were observed. In 'SDR', shading led to a significant increase in leaf area, longer branch lengths, and increases in bract length and width, indicating positive effects on growth. In contrast, 'ID' exhibited the opposite responses. Integrated multivariate analysis and correlation analysis revealed overall differences in the physiological responses to shading treatment between the two cultivars, and seven representative physiological indicators, which were related primarily to the leaf phenotype and chlorophyll content, were screened. Under the 50% shading treatment that lasted 60 days, 'SDR' exhibited better performance than 'ID', suggesting a possible advantage in shaded environments. This study systematically elucidated the effects of shading on the growth and physiological traits of *Bougainvillea*, providing preliminary evidence of its shade response and valuable theoretical support for the selection of shade-tolerant cultivars and the development of cultivation management practices. However, more comprehensive shading gradient treatments combined with analyses of additional physiological and biochemical parameters will be helpful for the systematic elucidation of the mechanisms underlying shade tolerance in *Bougainvillea*.

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