Effects of Shading on Photosynthetic Characteristics of Three Ranunculaceae Species and Shade Tolerance Evaluation: Postprint

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Abstract

To investigate the response mechanisms of three Ranunculaceae species—Ranunculus japonicus, Thalictrum fortunei, and Dichocarpus dalzielii—to different light environments, this study established five light gradient treatment levels (0%, 30%, 50%, 70%, and 90% shading degree) and measured the photosynthetic indices of the three species to examine the effects of different shading treatments on their photosynthetic characteristics and evaluate their shade tolerance. The results showed that with increasing shading degree: (1) The contents of chlorophyll a, chlorophyll b, chlorophyll (a+b), and carotenoids in the three species exhibited an upward trend, while the chlorophyll a/b ratio decreased. (2) The apparent quantum yield (AQY) of all three species first increased and then decreased; the maximum net photosynthetic rate (Pmax) of Ranunculus japonicus and Dichocarpus dalzielii showed a trend of first rising then falling, while that of Thalictrum fortunei exhibited a decreasing trend; the light saturation point (LSP), light compensation point (LCP), and dark respiration rate (Rd) of all three species gradually decreased. (3) The initial fluorescence (Fo) of the three species first decreased then increased, while the maximum fluorescence (Fm), variable fluorescence (Fv), PSII maximum photochemical efficiency (Fv/Fm), and PSII potential activity (Fv/Fo) values first increased then decreased; the quantum yield of heat dissipation (ϕDo) and energy dissipated per reaction center (DIo/RC) showed a trend of first decreasing then increasing, whereas the quantum yield of electron transport (ϕEo), light energy absorbed per reaction center (ABS/RC), light energy trapped per reaction center (TRo/RC), energy used for electron transport per reaction center (ETo/RC), photosynthetic performance index (PIabs), and comprehensive performance index (PItotal) exhibited a trend of first increasing then decreasing. (4) Comprehensive analysis of 20 individual indices was conducted using principal component analysis, membership function method, and other analytical methods, revealing the following shade tolerance ranking among the three species: Thalictrum fortunei > Dichocarpus dalzielii > Ranunculus japonicus. Based on these results, it is concluded that the three Ranunculaceae species possess different adaptive capacities to light, providing a basis for the application of Ranunculaceae plants in landscaping.

Full Text

Abstract

To investigate the response mechanisms of *Ranunculus japonicus*, *Thalictrum fortunei*, and *Delphinium anthriscifolium* var. *savatieri* to different light environments, this study established five shade treatment levels (0%, 30%, 50%, 70%, and 90% shade degree) and measured photosynthetic indicators to examine the effects of shading on photosynthetic characteristics and evaluate shade tolerance. The results showed that with increasing shade degree: (1) The contents of chlorophyll a, chlorophyll b, total chlorophyll (a+b), and carotenoids in all three species increased, while the chlorophyll a/b ratio decreased. (2) The apparent quantum efficiency (AQY) of all three species initially increased then decreased; the maximum net photosynthetic rate (Pmax) of *R. japonicus* and *D. anthriscifolium* var. *savatieri* showed a similar trend of initial increase followed by decrease, while that of *T. fortunei* declined continuously; the light saturation point (LSP), light compensation point (LCP), and dark respiration rate (Rd) of all three species gradually decreased. (3) Initial fluorescence (Fo) first decreased then increased, while maximum fluorescence (Fm), variable fluorescence (Fv), PSII maximum photochemical efficiency (Fv/Fm), and PSII potential activity (Fv/Fo) initially increased then decreased; the quantum ratio of heat dissipation (ϕDo) and energy dissipated per unit reaction center (DIo/RC) showed a pattern of initial decrease followed by increase, whereas electron transport quantum yield (ϕEo), light energy absorbed per unit reaction center (ABS/RC), light energy captured per unit reaction center (TRo/RC), energy used for electron transport per unit reaction center (ETo/RC), photosynthetic performance index (PIabs), and comprehensive performance index (PItotal) initially increased then decreased. (4) Comprehensive analysis of 20 individual indicators using principal component analysis and membership function methods revealed the following shade tolerance ranking: *T. fortunei* > *D. anthriscifolium* var. *savatieri* > *R. japonicus*. These results demonstrate that the three Ranunculaceae species possess different light adaptation capabilities, providing a scientific basis for their application in landscape greening.

Keywords: Ranunculaceae, shading, photosynthetic characteristics, shade tolerance, evaluation

Introduction

Light plays a crucial role in plant growth and development, not only influencing photosynthetic carbon assimilation but also providing essential energy for plant life (Wit et al., 2016). Light intensity affects photosynthesis and regulates plant growth through modifications in photosynthetic pigments, enabling plants to better adapt to environmental changes (Shi Yingying, 2020). Photosynthesis forms the foundation of plant growth, and shading can reduce leaf and soil temperatures while increasing soil moisture content, thereby promoting photosynthetic activity and organic matter accumulation (Chen Pei et al., 2010). Under reduced light intensity, plants typically employ strategies such as increasing chlorophyll content, lowering light compensation points and respiratory consumption, and enhancing quantum efficiency to improve adaptation to low-light conditions (Wang Yanan et al., 2020). With urbanization accelerating, increased building density and diversified layouts have created more shaded environments and complex light conditions in cities, making research on plant light response mechanisms practically significant for ecological urban construction (Yu Yingying et al., 2015).

The Ranunculaceae family comprises predominantly annual to perennial herbs with typically alternate or basal leaves. Widely distributed globally, this family concentrates in temperate and cold temperate regions. China hosts 42 genera and 720 species, mostly in southwestern mountainous areas (Liu Huijie et al., 2016; Mu Yingtong et al., 2022). Ranunculaceae species exhibit vibrant colors and diverse forms, offering high ornamental value. Some have been successfully applied in landscaping, and their rich chemical compositions also confer substantial medicinal value (Hu Lujie et al., 2015). Current research on Ranunculaceae primarily focuses on resource surveys and medicinal properties, with some studies addressing heat and drought tolerance, while shade tolerance research remains limited (Mo Jianbin et al., 2022; Zhang Lijuan et al., 2022). Studies on three Ranunculaceae species in the alpine meadows of the Qinghai-Tibet Plateau revealed that under shading, *Trollius farreri*, *Anemone obtusiloba*, and *Aconitum gymnandrum* adapt to low-light environments through reduced vegetative growth and decreased flower numbers (Meng Jinliu, 2010).

Ranunculus japonicus, *Thalictrum fortunei*, and *Delphinium anthriscifolium* var. *savatieri* are three herbaceous Ranunculaceae species with elegant forms, brilliant flowers, lush foliage, and early spring flowering, offering excellent prospects for landscape applications. These plants can enrich early spring urban vegetation, enhance native characteristics, and generate significant economic and social benefits. Current research on these species has primarily focused on chemical composition analysis (Zheng Wei, 2006), plant resource surveys (Xiao Haiming et al., 2019), chloroplast genomics, and phylogeny (Wang Yuanyuan et al., 2020), while shade tolerance studies remain unexplored, limiting their urban landscape application. Therefore, this study investigates the photosynthetic response mechanisms and compares shade tolerance among these three species to provide critical information for their landscape utilization.

Using field-transplanted specimens of the three species, this research measured chlorophyll content, photosynthetic response parameters, and chlorophyll fluorescence characteristics under shade stress. Principal component analysis and membership function analysis were employed to address: (1) the individual response strategies of the three Ranunculaceae species under different light conditions; (2) differences in light adaptation among the three species under varying shade intensities; and (3) comparative shade tolerance evaluation. The goal is to identify shade-tolerant Ranunculaceae species and provide theoretical support for their domestic application and promotion.

1.1 Experimental Materials

The experiment was conducted at the National Landscape Architecture Experimental Teaching Demonstration Center of Nanjing Forestry University (118°49 E, 32°05 N). Located in the lower Yangtze River region, the area features a subtropical monsoon climate with an average annual temperature of 16°C and average annual precipitation of 1,034 mm. In early January 2021, plants of *R. japonicus*, *T. fortunei*, and *D. anthriscifolium* var. *savatieri* (transplanted from Purple Mountain, Nanjing) were potted in plastic containers (21 cm diameter, 18 cm height) at two plants per pot, using a soil mixture of garden soil and nutrient substrate (2:1 ratio). All materials were placed in the demonstration center for acclimation under consistent water and fertilizer conditions to exclude confounding variables.

1.2 Experimental Design

Shade shelters were constructed using shade nets of different transmittance levels (3 m × 1.5 m × 1.5 m, spaced 5 m apart). Based on previous research, five light levels were established: full sunlight (CK, 1,500-1,600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), 30% shade (T1, 1,000-1,100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), 50% shade (T2, 700-750 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), 70% shade (T3, 400-450 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and 90% shade (T4, 100-120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Tian Linlin et al., 2019). Each treatment comprised three replicates of 15 pots each, totaling 675 pots across the three species. The experiment commenced on March 1, 2021. Based on preliminary results showing severe growth inhibition in some Ranunculaceae plants after 40 days of shading, fresh leaves were collected at 35 days for chlorophyll content measurement (8:00 AM) and light response curves and chlorophyll fluorescence parameters (9:00-11:00 AM).

1.3 Measurement Methods

1.3.1 Chlorophyll Content Determination From each treatment, three healthy seedlings were randomly selected. The third to fifth fully expanded, healthy leaves from the main branch were collected, cleaned, cut into small pieces, and mixed. Following Li (2020), 0.05 g samples were placed in 10 mL centrifuge tubes with 10 mL of 80% acetone, extracted in darkness at 4°C with shaking every 6 hours until leaves turned white. Absorbance was measured at 663 nm, 646 nm, and 470 nm using a Lambda 365 UV spectrophotometer (PerkinElmer, USA).

1.3.2 Photosynthetic-Light Response Parameter Measurement Three healthy seedlings per treatment were randomly selected using the same leaf criteria. Between 9:00-11:00 AM on clear, windless days, a CIRAS-3 portable photosynthesis system (PP-system, USA) measured net photosynthetic rate (Pn) across 13 photosynthetically active radiation (PAR) gradients: 1,800, 1,600, 1,400, 1,200, 1,000, 800, 600, 400, 200, 100, 50, 25, and 0 $\mu\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$. Light response curves were fitted using Ye Zipiao' s modified rectangular hyperbola model to calculate maximum net photosynthetic rate (Pmax), light saturation point (LSP), light compensation point (LCP), apparent quantum efficiency (AQY), and dark respiration rate (Rd). Measurements were conducted at CO_2 concentration of 380-420 $\mu\mathrm{mol} \cdot \mathrm{mol}^{-1}$, leaf temperature of 25°C, and leaf chamber humidity of 80%. Each parameter was measured three times and averaged.

1.3.3 Chlorophyll Fluorescence Parameter Measurement Three healthy seedlings per treatment were selected following the same leaf criteria. Between 9:00-11:00 AM on clear, windless days, a Handy PEA plant efficiency analyzer (Hansatech Instruments, UK) measured fluorescence parameters after 20 minutes of dark adaptation. Each parameter was measured three times and averaged.

1.4 Data Analysis

Data were organized using Excel 2010 and analyzed with SPSS 25.0. Chlorophyll fluorescence parameters were processed using PEAPlus software. Following established methods (Luo Yao et al., 2013; Shi Yingying, 2020), principal component analysis and membership function analysis evaluated shade tolerance.

The shade tolerance coefficient (α) was calculated as: α = measured value at 70% shade / measured value in control.

Membership function: u(Xi) = (Xi - Xmin) / (Xmax - Xmin)

Comprehensive evaluation value (D) was calculated by summing the products of membership function values and their respective weights.

Where Xi represents the ith comprehensive indicator, Xmin and Xmax are its minimum and maximum values, Wi is the weight of the ith comprehensive indicator, and Pi is its contribution rate. The D value represents the comprehensive shade tolerance evaluation. Higher D values indicate greater shade tolerance.

Results

2.1 Effects of Shading on Leaf Chlorophyll Content

As shown in [Figure 1: see original paper], chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl a+b), and carotenoid (Car) contents in all three species increased with shading intensity, consistently ranking as: *T. fortunei* > *D. anthriscifolium* var. *savatieri* > *R. japonicus*. All treatments differed significantly in *R. japonicus*, while shaded treatments differed significantly from the control in the other two species. The Chl a/b ratio decreased with shading, with significant differences between shaded treatments and the control in *T. fortunei* and *D. anthriscifolium* var. *savatieri*.

2.2 Effects of Shading on Photosynthetic-Light Response Parameters

The light response curves of all three species showed a parabolic shape ([Figure 2: see original paper]). When PAR was below 400 μmol · m^{-2} · s^{-1}, Pn increased rapidly with PAR; between 400-800 μmol · m^{-2} · s^{-1}, the increase slowed; above 800 μmol · m^{-2} · s^{-1}, Pn plateaued or declined.

presents the photosynthetic parameters. AQY initially increased then decreased in all species, peaking at 30% shade for *R. japonicus* and *T. fortunei* and at 50% shade for *D. anthriscifolium* var. *savatieri*. Pmax followed a similar trend for *R. japonicus* and *D. anthriscifolium* var. *savatieri*, while *T. fortunei* showed a continuous decline. LSP, LCP, and Rd all decreased with increasing shade.

2.3 Effects of Shading on Chlorophyll Fluorescence Characteristics

2.3.1 Fast Chlorophyll Fluorescence Parameters As shown in , initial fluorescence (Fo) first decreased then increased with shading intensity in all species. Maximum fluorescence (Fm), variable fluorescence (Fv), PSII maximum photochemical efficiency (Fv/Fm), and PSII potential activity (Fv/Fo) initially increased then decreased, generally peaking at T3 (70% shade) and differing significantly from the control.

2.3.2 Energy Distribution Ratios As shown in [Figure 3: see original paper], the quantum ratio of heat dissipation (ϕDo) decreased then increased with shading, reaching minimum values at T3 (17.10%, 18.04%, and 20.10% below control, respectively) and increasing at T4 but remaining below full sunlight levels. Electron transport quantum yield (ϕEo) showed the opposite trend, peaking at T3 (17.31%, 31.10%, and 8.71% above control, respectively).

2.3.3 PSII Reaction Center Activity Parameters As shown in [Figure 4: see original paper], light energy absorbed per unit reaction center (ABS/RC) initially increased then decreased, peaking at T3 for *R. japonicus* and *D. anthriscifolium* var. *savatieri* and at T2 for *T. fortunei* (17.02%, 8.04%, and 29.19% above control, respectively). Energy dissipated per unit reaction center (DIo/RC) showed the opposite pattern, reaching minimum values at T3 for *R. japonicus* and *D. anthriscifolium* var. *savatieri* and at T2 for *T. fortunei* (30.47%, 24.86%, and 26.74% below control, respectively). Light energy captured per unit reaction center (TRo/RC) and energy used for electron transport per unit reaction center (ETo/RC) both initially increased then decreased, with *R. japonicus* peaking at T2 and the other two species at T3.

2.3.4 Photosynthetic Performance Indices The photosynthetic performance index (PIabs) and comprehensive performance index (PItotal) reflect reaction center activity and energy conversion efficiency under stress. As shown in [Figure 5: see original paper], PIabs initially increased then decreased, peaking at T3 for *R. japonicus* and *D. anthriscifolium* var. *savatieri* (74.08% and 42.63% above control, respectively) and at T2 for *T. fortunei* (82.83% above control). PItotal showed a similar pattern, peaking at T3 for *R. japonicus* and *D. anthriscifolium* var. *savatieri* and at T2 for *T. fortunei* (48.80%, 87.94%, and 37.41% above control, respectively).

2.4 Comprehensive Shade Tolerance Evaluation

Twenty indicators were analyzed using principal component analysis, which extracted four independent components explaining 91.474% of total variance (). The first component (44.909% variance) included Chl a, Chl b, Chl a+b, Car, Fm, Fv, Fv/Fm, Fv/Fo, ϕDo, ϕEo, TRo/RC, and PIabs. The second component (22.468% variance) comprised Chl a/b, AQY, Fo, and DIo/RC. The third component (15.755% variance) included ϕEo, ABS/RC, and PItotal. The fourth component (8.342% variance) consisted of Rd. The comprehensive weights were 0.491, 0.246, 0.172, and 0.091, respectively. Based on D values, the shade tolerance ranking was: *T. fortunei* (0.804) > *D. anthriscifolium* var. *savatieri* (0.420) > *R. japonicus* (0.091) ().

Discussion

3.1 Effects of Shading on Chlorophyll Content

Photosynthetic pigments serve as carriers for photosynthesis, absorbing, transferring, and converting light energy while influencing plant growth (Jin Yaqin et al., 2011). Chlorophyll content reflects light capture capability, while carotenoids provide photoprotection and light harvesting, both affecting stress adaptation (Zeng Xiangyan et al., 2021; Liu Bao et al., 2011). The observed increase in chlorophyll and carotenoid contents with shading indicates that these plants enhance light capture to adapt to low-light conditions while protecting photosynthetic apparatus from excess energy (Bell & Danneberger, 1999; Lichtenthaler et al., 2007). However, *T. fortunei* showed decreased Chl a and total chlorophyll at 90% shade, suggesting that excessive shading reduces photosynthetic pigment synthesis and weakens adaptation. A low Chl a/b ratio indicates shade tolerance, as plants increase Chl b content to capture more light and improve energy utilization under low light (Zhao Shun et al., 2014). The decreasing Chl a/b ratios in all three species confirm this adaptive strategy, consistent with studies on *Aglaonema commutatum* and *Polygonatum cyrtonema* (Zheng Xueyan et al., 2022; Liang Yongfu et al., 2019).

3.2 Effects of Shading on Photosynthetic Response Parameters

Apparent quantum efficiency (AQY) reflects photosynthetic capacity under weak light, with higher values indicating better light utilization (Yang Liting et al., 2022). The initial increase then decrease in AQY across all species, peaking at 30% shade for *R. japonicus* and *T. fortunei* and 50% shade for *D. anthriscifolium* var. *savatieri*, demonstrates adaptive enhancement of light use efficiency under moderate shading. Maximum net photosynthetic rate (Pmax) indicates maximum photosynthetic capacity, with higher values enabling greater conversion of light energy to chemical energy to support growth under low light (SHARP et al., 1984; Li Donglin et al., 2019). The peak Pmax values at 30% shade for *R. japonicus* and under full light for the other two species indicate their capacity for vigorous photosynthesis under full or moderate light, consistent with research on *Phoebe bournei* seedlings (Wang Zhenxing et al., 2012). Light saturation point (LSP) and light compensation point (LCP) directly reflect weak-light utilization capacity and are important shade tolerance indicators. Low LCP enables effective photosynthesis under weak light, while low LSP allows rapid attainment of maximum photosynthetic efficiency (Zhang Zhe et al., 2013). The decreasing LSP and LCP with shading indicate enhanced photosynthetic efficiency at lower light intensities, supporting organic matter accumulation and energy requirements (Liu Huimin et al., 2016). Dark respiration rate (Rd) typically decreases with light intensity, helping maintain stable dry matter accumulation when photosynthesis is reduced (Wang Zhenxing et al., 2012), a pattern observed in all three species.

3.3 Effects of Shading on Chlorophyll Fluorescence Characteristics

Initial fluorescence (Fo) reflects energy dissipation through fluorescence and heat; increased Fo under stress indicates thylakoid membrane damage and PSII reaction center inactivation (Liang Fang et al., 2010; Huang Qiuxian et al., 2015). The increase in Fo at 90% shade for *R. japonicus* and 70% shade for the other two species suggests that excessive shading causes irreversible damage or reversible inactivation of PSII reaction centers. Maximum fluorescence (Fm) reflects electron transport potential of PSII reaction centers. The initial increase then decrease in Fm, peaking at 70% shade, indicates optimal electron transport efficiency under moderate shading but reduced photosynthesis under excessive shade (Du Lan et al., 2019). Under stress, increased Fv/Fm and Fv/Fo reflect enhanced conversion of light energy to chemical energy, improving photosynthetic function (Liu Yueqiu et al., 2017). The pattern of initial increase then decrease, peaking at 70% shade, demonstrates adaptive capacity to weak light, with subsequent declines indicating intolerance to excessive shading, consistent with studies on *Physocarpus opulifolius* 'Lutein' and *Borago officinalis* (Liang Wenhua et al., 2018; Tian Linlin et al., 2019).

Under shading, decreased quantum ratio of heat dissipation (ϕDo) and increased electron transport quantum yield (ϕEo) indicate reduced energy loss and enhanced electron transport. In this study, ϕDo decreased and ϕEo increased except under 90% shade, demonstrating that all three species can adjust energy distribution in PSII reaction centers to adapt to environmental changes (Jia Hao et al., 2015). The parameters ABS/RC, TRo/RC, and ETo/RC reflect QA reduction state activity in PSII reaction centers. Their increase with shading, peaking at 70% shade, indicates relatively high energy utilization efficiency under appropriate shading (Huang Qiuxian et al., 2015). Conversely, DIo/RC decreased then increased with shading, reaching maximum values under full light, indicating that these plants dissipate excess energy through heat dissipation mechanisms under strong light to protect the photosynthetic system. Moderate shading effectively reduces this energy loss, while excessive shading increases energy dissipation (Wilson et al., 2006; Tian Linlin, 2019). PIabs and PItotal, representing energy conversion efficiency based on absorbed light, directly affect plant performance under adverse conditions (Yusuf et al., 2011). Their initial increase then decrease with shading indicates that moderate shading promotes efficient light capture and electron transport, improving energy conversion efficiency (Liu Yingjiao, 2015).

3.4 Comprehensive Shade Tolerance Evaluation

Principal component analysis combined with membership function evaluation provides a more comprehensive assessment than single indicators. This study examined photosynthetic indicator changes under shade stress, converted them to shade tolerance coefficients, and extracted four principal components explaining 91.474% of total variance. The D value, representing comprehensive shade tolerance, ranked the three species as *T. fortunei* (0.804) > *D. anthriscifolium* var. *savatieri* (0.420) > *R. japonicus* (0.091), with *T. fortunei* showing the strongest shade tolerance and suitability for low-light environments.

In conclusion, the three Ranunculaceae species adjust chlorophyll content, photosynthetic response parameters, and chlorophyll fluorescence characteristics to adapt to reduced light intensity, though their adaptive capacities differ. The comprehensive evaluation indicates that *T. fortunei* possesses the strongest shade tolerance, suitable for shaded environments such as sparse woodlands, building shadows, and under urban overpasses. The other two species have moderate shade tolerance and require more restricted planting ranges. Scientific consideration of these differential photosynthetic responses under varying light conditions is essential for successful landscape application and promotion of these species.

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