Effects of light quality on leaf growth and photosynthetic fluorescence of *Brasenia schreberi* seedlings

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**A B S T R A C T**

*Brasenia schreberi* J. F. Gmel, a perennial floating-leaved macrophyte with high economic value as an aquatic vegetable, has been listed as first-class endangered species in China, mainly due to its habitat loss. Protected cultivation is a potential strategy to meet the demand of both plant conservation and vegetable market, whereas pre-experiments are still needed before series of parameters can be properly set for the large-scale growth of the plants indoor. Light quality is one of the major factors controlling the development of plants and consequently becomes an important factor when planting *B. schreberi* indoor. This experiment used three artificial light sources to investigate the response of *B. schreberi* seedlings to different light qualities, including the red-blue LED light (red: blue = 5:1, RB-LED), the white LED light (W-LED) and the white fluorescent (W-Fluo). Our results indicated that the responses of *B. schreberi* towards varied light qualities differed from those of most terrestrial plants. The total leaf number of the RB-LED treatment was the highest; the number of the submerged leaf and the rolled leaf of the RB-LED treatment was higher than that of the other two treatments, but the number of floating leaves was the lowest. Both the specific leaf weight and the pigment contents per unit leaf area were the lowest in the RB-LED treatment.

1. Introduction

*Brasenia schreberi* J. F. Gmel is a perennial floating-leaved macrophyte in the Nymphaeaceae family (also listed in the Cabombaceae family) (Yu, 1991), distributed in Southeast Asia, Europe, North America, Australia and some other regions (See Figure 1 for the natural habitat of *B. schreberi* and its floating, rolled and submerged leaves). It is an aquatic vegetable with high economic value in China. The underwater organs of the plant are wrapped by a thick mucilage mainly composed of polysaccharides, including galactose, mannose, trehalose, rhamnose, xylose, arabinose, etc (Kakuta and Misaki, 1979; Feng et al., 2019). The mucilage has strong antioxidant capacity which may enhance human immunity, reduce blood sugar and plasma cholesterol. Also, its zinc rich characteristic may prevent the occurrence of ADHD in children (Li et al., 2018). As a traditional aquatic vegetable in China, *B. schreberi* has a long history of cultivation in Suzhou of Jiangsu Province and Hangzhou of Zhejiang Province in east China, but the main cultivation areas have been transferred to Lichuan of Hubei Province and Shizhu of Chongqing Municipality in central China. The growth of *B. schreberi* requires good water quality and nutrient-enriched sediments (Xie et al., 2018a). With severe deterioration and degradation of wetlands, *B. schreberi* has been listed as an endangered species and its wild distribution area has shrunk sharply. In addition, recent studies have demonstrated that different *B. schreberi* populations in China have low levels of genetic diversity, which is unfavorable for its protection (Zhang and Gao, 2008; Liu et al., 2012; Li et al., 2018).

With rapid expansion of Chinese food market, indoor protected cultivation of vegetables has been considered as an efficient way in replacing the traditional outdoor cultivation, the latter is restricted due to farm land deficiency. We suppose that protected cultivation can be a potential strategy to meet the demands of *B. schreberi* for both the species conservation and the vegetable market. However, instead of the highly...
developed indoor culture of terrestrial vegetables, that of aquatic vegetables has been scarcely attempted. Compared with the wild situation, the indoor growth of B. schreberi is quite different in morphological development, even unable to complete the life cycle.

Light is an important environmental regulator in protected cultivation. Light quality has effects on plant physiological metabolism, gene expression, photoperiod response, and photomorphogenesis, etc (Zheng et al., 2019a; De Keyser et al., 2019; Park et al., 2015). Plants can detect subtle changes in light and initiate changes in the physiological and morphological structures necessary for their survival (Hogewoning et al., 2010; Xu et al., 2015). Light-emitting diode (LED) has become a new light source in protected cultivation because of its advantages of energy saving, long service life and precise modulation of spectrum (Hernandez and Kubota, 2016; Tennesen et al., 1994). Researches on LED light quality was focused on crops in earlier stage (Zheng et al., 2019b; Goins et al., 1997), but have been switched to fruits, vegetables, flowers, etc. recently, such as pomegranates (Bantis et al., 2018), gabirobas (Centofante, 2019), hydroponic lettuces (Yan et al., 2019), and phalenopopsis (Ren et al., 2016), which are of higher economic value.

Red light can increase plant pigment contents, increase leaf area, and facilitate the accumulation of photosynthetic products (Xu et al., 2015); blue light can promote stomatal opening and increase photosynthetic rate (Sharkey and Raschke, 1981). However, in recent years, studies have shown that the response of plants to different light qualities varied among species, tissues and organs (Liu et al., 2018). In addition, although there are many reports on the cultivation of terrestrial plants and their response to light quality, few studies have been focused on aquatic plants. It is not clear whether the response of aquatic plants to different light qualities is the same as that of terrestrial plants.

We suspect that the responding mechanism of B. schreberi to varied light sources may be different to that of terrestrial plants, thus a proper light source becomes the first issue that need to be decided for its protected cultivation. Instead of the light intensity that has been well studied, we focused on the light quality in this paper. Three commonly used artificial light sources were explored for the indoor growth of the overwintering buds of B. schreberi. Through the analysis of leaf characteristics, pigment contents, chlorophyll fluorescence and relative photosynthetic indicators, the study is expected to provide a reference for the selection of light sources in the protected cultivation of B. schreberi.

2. Material and method

2.1. Experimental design

Three commonly used artificial light sources: red and blue LED (RB-LED, R: B = 5:1), white LED (W-LED) and white fluorescent (W-Fluo) were tested in the experiment. The light intensity was maintained as 120 ± 30 μmol m⁻²·s⁻¹, which was a mean value of light intensity measured at the surface of both water and mud, with a photoperiod of 12 h/12 h, light/dark. Room temperature was set constantly at 25 ± 2 °C. Each of the light quality treatments had 36 cups of the plants as replication. To ensure the uniformity of light received by different plants, the location of each cup in the water tank was adjusted every 2 d between center and edge of the tank.

2.2. Plant materials

Overwinter buds of B. schreberi were collected at the end of March 2018 in Suzhou, Jiangsu Province. Healthy buds of similar size were selected and transplanted, as one bud per cup, into white translucent hard plastic culture cups (8 cm in diameter and 8 cm in depth) filled with fresh river mud. Then the culture cups with overwinter buds were moved into the bottom of water tanks with 500 × 380 × 250 mm (length × width × height) in size. During the experiment, the water level was maintained about 20 cm above the mud surface, and 5 mL of double strength Hoagland nutrient solution (Hoagland and Arnon, 1950) was injected into each cup every 7 d (3 cm in depth below mud surface) to make sure enough nutrients for growth.

2.3. Leaf characteristics and pigment measurements

After growth for 20 d, the numbers of floating leaves, submerged leaves and rolled leaves from each cup were counted. After 40 d, 7 largest floating leaves from each light treatment were harvested, weighed for the fresh weight of each leaf (M), scanned to obtain the single leaf area (S), and then the specific leaf weight was calculated as SLW = M/S (Mishanin et al. 2016). The pigments of the same leaf samples were extracted by 80% acetone after rapid homogenization, and the concentrations of chlorophyll a (Chl a), chlorophyll b (Chl b) and carotenoid (Cars) were measured by UV-2800A spectrophotometer (UNICO, USA), using the method of Lichtenthaler and Wellburn (1983).

2.4. Chlorophyll fluorescence measurements

Fully developed floating leaves were selected for chlorophyll fluorescence measurements. The Fm and Fo values were measured using MINI-PAM (WALZ, Germany) after 30 min of dark adaption. The selected leaves were then exposed to their original growing lights for more than 30 min to ensure fully light adaption, after which auto-light induction curves were maintained at the same site, with series of Fm′, Fo′ and Fv/Fm values being recorded. According to the formulas of Maxwell and Johnson (2000), the maximum photochemical efficiency of photosystem II (PSII) ΦPSII = (Fm′−F0′)/Fm′ and the actual photochemical quantum yield of PSII under photactivation conditions ΦPSII = (Fm′−F0′)/Fm′, electron transport rate ETR = Fv/Fm×PAR×0.5×0.84 (PAR is real-time light intensity in μmol·m⁻²·s⁻¹), photochemical quenching qP = (Fm′−F0′)/(Fm′−F1′) and non-photochemical quenching NPQ = (Fm−Fm′)/Fm′ were calculated. The measurement of maximum photochemical efficiency after dark adaptation was repeated for 10 samples for...
each growth condition, while the rest parameters with induction curves were repeated for 7 samples.

Based on the Ralph and Gademann (2005) curve fitting model and the exponential decay equations of ETR = \( P_0 \times (1 - e^{-\alpha \times \text{PAR}/P_{0}}) \times e^{-\beta \times \text{PAR}/P_{0}} \), ETR\(_{\text{m}}\) = \( P_0 \times (\alpha/(\alpha + \beta)) \times (\beta/(\alpha + \beta))^{\beta/\alpha} \), the initial slope (\( \alpha \)) and photoinhibition coefficient (\( \beta \)), maximum potential electron transfer rate (\( P_0 \)), maximum electron transport rate (ETR\(_{\text{m}}\)), minimum saturating irradiance (\( E_k \)) and saturating irradiance (E\(_{\text{m}}\)) were further calculated. Here to unify the calculation process, we used the original ETR values (ETR = \( \Phi_{\text{PSII}} \times \text{PAR} \times 0.5 \times 0.84 \)) directly to replace the rETR values (rETR = \( \Phi_{\text{PSII}} \times \text{PAR} \)) in the Ralph and Gademann equation (Xie et al., 2018b; Ye et al., 2013).

### 2.5. Statistical analyses

The data were statistically analyzed using SPSS 22. Among different treatment groups, the number of leaves, leaf area, specific leaf weight, maximum photochemical efficiency after dark adaptation, ETR curve fitting parameters and the leaf pigment contents were analyzed by one-way ANOVAs, and multiple comparisons were performed by LSD tests; Fluorescence-induced curves (\( \Phi_{\text{PSII}}, \text{ETR}, \text{qP} \) and NPQ) were compared using paired data T-test. Effects were considered statistically significant at \( P < 0.05 \).

### 3. Results

#### 3.1. Effects of different light qualities on leaf number of B. schreberi seedlings

After 20 d of cultivation, the number of floating leaves in RB-LED only accounted for 6% of the total number of leaves, and was significantly lower than that of the W-LED (\( P < 0.05 \), Figure 2a), which accounted for 16% of the total number of leaves. Under all three light quality treatments, the proportion of submerged leaves in the total number of leaves is more than 75%. The number of submerged leaves in the RB-LED treatment was significantly higher than those in the W-LED and W-Fluo treatments (\( P < 0.05 \), Figure 2b). The number of submerged leaves in W-LED was slightly lower than that in W-Fluo (\( P > 0.05 \), Figure 2c). The number of rolled leaves in RB-LED and W-Fluo was similar (\( P > 0.05 \)), accounting for 13% and 14% of the total number of leaves respectively. W-LED has the least amount of rolled leaves which accounted for 9% of the total number (\( P > 0.05 \)). The total leaf number of RB-LED treated seedlings was significantly higher than those of W-LED and W-Fluo treatments (\( P < 0.05 \), Figure 2d). The total leaf number of W-LED treatment was lower than that of the W-Fluo treatment (\( P > 0.05 \)).

#### 3.2. Effects of different light qualities on leaf area and specific leaf weight

After 40 d of cultivation, the single leaf area and SLW of the floating leaves in different light quality treatments also showed some differences (Table 1). The leaf area of the floating leaves in the white fluorescent treatment was significantly larger than that in the W-LED treatment (\( P < 0.05 \)). The W-Fluo treatment had the largest SLW, the RB-LED treatment had the smallest, and the differences among the three light quality treatments were significant (\( P < 0.05 \)).

#### 3.3. Effects of different light qualities on photosynthetic pigment contents

It was found that the photosynthetic pigment contents of the three light quality treatments were different under the measurement of per unit leaf area and per unit fresh leaf weight (Figure 3). Under the fresh weight measurement mode, the total chlorophyll contents of the W-LED treatment were higher than those of the other two treatments, the difference was mainly reflected in Chl a (\( P < 0.05 \)) instead of Chl b (\( P > 0.05 \)). There was no difference in the total chlorophyll contents, Chl a and Chl b contents between RB-LED and W-Fluo under the fresh weight measurement mode (\( P > 0.05 \)). However, under the leaf area measurement mode, the total chlorophyll contents and Chl a content of W-LED and W-Fluo were significantly higher than those of the RB-LED treatment (\( P < 0.05 \)), and no difference was shown between the two white light sources (\( P > 0.05 \)). The carotenoid contents under the three treatments also showed similar changes. The W-LED treatment was significantly higher than the other two treatments under the leaf weight measurement mode (\( P < 0.05 \)). In comparison, two white light treatments were significantly different.
higher than the RB-LED treatment under the leaf area measurement mode ($P < 0.05$).

Regarding the relative proportions of different pigment compositions, the ratio of Chl a/b from high to low was RB-LED > W-LED > W-Fluo ($P > 0.05$, Figure 3e). As for the ratio of chlorophylls to carotenoids, the RB-LED treatment was slightly higher than two white light treatments ($P > 0.05$, Figure 3f).

### Table 1. Leaf area and specific leaf weight of *Brasenia schreberi* under three light quality treatments.

| Treatments           | Leaf area (cm$^2$) | Specific leaf weight (gFW*m$^{-2}$) |
|----------------------|-------------------|-----------------------------------|
| Red-blue LED        | 23.35 ± 1.53ab    | 1.53ab                            |
| White LED           | 19.59 ± 1.80b     | 1.80b                             |
| White fluorescent   | 27.69 ± 2.17a     | 2.17a                             |

Mean ± SE, n = 7; Different lowercase letters indicate significant differences among three light quality treatment group ($P < 0.05$).

### 3.4. Effects of different light qualities on chlorophyll fluorescence parameters

The maximum photochemical efficiency of *B. schreberi* floating leaves was measured after dark adaptation. It was found that the $F_{v}/F_{m}$ values were higher than 0.8 under the three light quality treatments ($P > 0.05$, Figure 4), indicating all plants were relatively healthy and no obvious stress happened during cultivation.

Differences were shown on the light induction curves among the three different light quality treatments (Figure 5). Under the same measurement light intensity, the $\Phi_{PSII}$ value of the floating leaves was the highest under white fluorescent treatment, followed by W-LED and RB-LED and the differences among these three groups were significant ($P < 0.05$, Figure 5a). The effect of different light qualities on ETR was more obvious than that of $\Phi_{PSII}$. Under the medium and high measurement light intensity, the ETR values of the RB-LED treatment were only about 2/3 of that of the W-Fluo treatment ($P < 0.05$). The ETR values of the W-LED treatment were in the middle, and the difference was also significant ($P < 0.05$, Figure 5b). The $qP$ values under different light quality
treatments showed similar trends with \( \Phi_{PSII} \). It also showed that the \( \Phi_P \) values of the W-Fluo treatment were relatively high, followed by the W-LED treatment, and the RB-LED treatment was the lowest (\( P < 0.05 \), Figure 5c). The trend of NPQ was reversed. Although the magnitude of the difference is relatively small, the NPQ values of the RB-LED treatment is obviously higher under medium and high measurement light intensity, followed by the W-LED and W-Fluo treatment. Statistical analysis showed that the NPQ values of the W-Fluo treatment were significantly different from the two LED treatments (\( P < 0.05 \), Figure 5d), but the difference between the two LED treatments was not significant (\( P > 0.05 \)).

### 3.5. ETR curve fitting analysis

The ETR curves of the \( B. \) schreberi floating leaves can be well fitted by the exponential decay equation (\( R^2 > 0.989 \)). Although the \( \alpha \) values, \( E_k \) values and \( E_m \) values of the three light quality treatments showed no significant difference (\( P > 0.05 \)), it was still obvious that these three derived parameters followed the order of RB-LED < W-LED < W-Fluo (Table 2). The \( P_s \) and ETR\(_{max} \) shared the same trend and these values of the RB-LED treatment were 68% of the W-Fluo treatment (\( P < 0.05 \)). The \( P_s \) value and ETR\(_{max} \) of the W-LED treatment were 90% and 88% of the W-Fluo treatment, respectively. The photoinhibition coefficient \( \beta \) of each light quality treatment was less than 0.01 (\( P > 0.05 \)).

### 4. Discussion

Plants can sense subtle changes in light quality through photoreceptors, which in turn regulate growth and development of plants through exciting signaling pathways (Ward et al., 2005). Leaf chlorophylls are responsible for the absorption, transmission, and transformation of light energy, while carotenoids take functions on both light energy capture and light damage defense (Sun et al., 2010). Based on the consideration of indoor protected cultivation, low light treatment was designed in the early stage of the experiment. The average light intensity in this experiment was much lower than that of natural sun radiation in the field. The pigment contents of the floating leaves showed similar characteristics of shade plants (Lichtenthaler et al., 2007). We have also analyzed the floating leaves of \( B. \) schreberi grown under natural light in the field (Xie et al., 2018b). Under the low light treatment, SLW, chlorophyll contents per unit leaf area and carotenoid contents per unit leaf area of \( B. \) schreberi leaves were only about 60% of those in the field, and the ratio of Chl \( a/b \) was only about 50% of that in the field. Our results were similar with what Bartucca et al. (2020) found that einkorn had lower levels of chlorophylls and carotenoids contents under a high proportion of red-light treatment compared with that under wide wavelength treatment. However, the photosynthetic pigments contents per unit fresh weight and the ratio of chlorophylls to carotenoids were almost the same as those in the field. Therefore, on the one hand, we believe that this is a
certain self-regulation of *B. schreberi* leaves adapting to low light environment; on the other hand, due to the change of specific leaf weight with different light quality, which we used as an index of leaf thickness, we believe that the pigment contents per unit area may be more proper than that of the traditional unit per leaf mass for the analysis of leaf photosynthetic function.

Red and blue light sources are common in the current indoor protected cultivation. Our study showed that the contents of chlorophylls and carotenoids in the *B. schreberi* floating leaves under the treatment of 5:1 RB-LED were lower than that of the white light treatments. Red light is believed to increase anthocyanins, chlorophylls and carotenoids, but most evidence comes from terrestrial plants (Xu et al., 2015). In recent years, there have been reports of red light and white light that are not conducive to pigment accumulation and photosynthetic efficiency (Liu et al., 2018). We are not sure whether the phenomenon we observed is common in aquatic plants, but the specific response of different plants to different light qualities is obvious. In addition, studies on Phalaenopsis showed that red light is not conducive to the accumulation of chlorophylls, while blue light is conducive to the accumulation of chlorophylls (Ren et al., 2016). It is unknown whether increasing the proportion of the blue light in the RB-LED treatment can improve the pigment accumulation in the floating leaves of *B. schreberi*.

Chlorophyll fluorescence parameters are often used as effective probes for studying the photosynthetic physiological state of plants. The *F₀/Fₘ* values measured after dark adaptation can effectively reflect the intrinsic light energy conversion ability of PSII reaction center. Several studies showed that light quality has significant effects on chlorophyll fluorescence parameters in leaves of plantlets. *Cunninghamia lanceolata* had higher levels of *F₀/Fₘ* and ETR values under a composite light with red, blue, purple, and green (Xu et al., 2020). The *Fₘ/Fₘ* and ETR of *Dendrobium candidum* plantlets under red and blue light were also found higher than under monochrome light (Wang et al., 2017). In our experiment, the *F₀/Fₘ* values of *B. schreberi* floating leaves under the three light quality treatments were all larger than 0.8, indicating that plants in this experiment were not under stress condition and hence generally healthy. However, the change of pigment ratio will affect the structure and stability of photosynthetic membrane of plant leaves, which will further affect other physiological processes related to photosynthesis in plants (Ramalho et al., 2002). Different light qualities can also affect the stomatal dynamic behaviour which will further affect the performance of photosynthesis in plants (Matthews et al., 2020). According to the light induction curve, the *Φₚₛₛᵢₙ* ETR, *q*P, and *P*ₑ values derived from ETR curves of the RB-LED treatment were lower than those of the white light treatments, but the NPQ increased slightly, indicating that the photochemical efficiency and ETR of the PSII reaction center are relatively weak under the red and blue light sources, which should be related to the decrease of chlorophyll contents (Chen et al., 2014). Based on the theory of Ralph and Gademann, *Eₗ* reflects the utilization of light energy by plants, which is related to fluorescence quenching. When *PAR < Eₗ*, photochemical quenching is dominant; when *PAR > Eₗ*, non-photochemical quenching is dominant. In the experiment, the *Eₗ* values of the three groups were higher than the light intensity received by the surface of the leaves, and the light energy was mainly utilized by fluorescence quenching (Ralph and Gademann, 2005). In the experiment, the NPQ value of the RB-LED treatment was slightly higher than those of the white light treatment groups, which should be a self-protection mechanism for the high light stress (Ruban, 2016). However, in view of the long-term cultivation in low light environment, we suppose that this NPQ-based protection mechanism has little contribution for the *B. schreberi* growth in the experiment.

| Treatment      | *a*     | *b*     | *Pₘ* (μmol e⁻ m⁻² s⁻¹) | Eₘ (μmol e⁻ m⁻² s⁻¹) | Eₛ (μmol e⁻ m⁻² s⁻¹) | Eₛₚₛᵢₙ (μmol e⁻ m⁻² s⁻¹) |
|----------------|---------|---------|------------------------|----------------------|----------------------|---------------------------|
| Red-blue LED   | 0.150 ± 0.0151a | 0.003 ± 0.0010a | 58.9 ± 9.2b          | 52.9 ± 8.0b          | 344.1 ± 35.4a          | 1734.2 ± 262.9a           |
| White LED      | 0.165 ± 0.0193a | 0.006 ± 0.0019a | 78.2 ± 4.8ab         | 67.9 ± 4.7ab         | 431.5 ± 40.1a          | 2082.5 ± 466.6a           |
| White fluorescent | 0.190 ± 0.0275a | 0.005 ± 0.0020a | 87.0 ± 5.0a          | 77.4 ± 3.9a          | 445.0 ± 46.4a          | 2159.9 ± 351.5a           |

*a*: Initial slope; *b*: Photoinhibition coefficient; *Pₘ*: Maximum potential electron transport rate; Eₘ: Maximum electron transport rate; Eₛ: Minimum saturating irradiance; Eₛₚₛᵢₙ: Saturating irradiance. Different lowercase letters indicate significant differences among the three light quality treatment groups (*P* < 0.05).

5. Conclusion

Under artificial light conditions, the total leaf number of *B. schreberi* seedlings treated with the RB-LED was higher than that of the W-LED and W-Fluo treatments, but the development of petioles was limited, so that most leaves could not reach out of the water surface. The chlorophyll contents and carotenoid contents per unit leaf area of floating leaves treated with the RB-LED were lower than those of white light treatments. *F₀/Fₘ* under dark adaptation showed that the plants were still in a healthy state, but according to the light induction curves, *Φₚₛₛᵢₙ*, ETR, *q*P, and *P*ₑ values derived from ETR curves of the RB-LED treatment were lower than those of the white light treatments, only NPQ was higher. This was not the
same with the results of most terrestrial plants. However, red and blue light sources can be properly used to increase the yield of buds and rolled leaves, together with a white light source to ensure sufficient accumulation of photosynthetic products. In addition, the application of white fluorescent light source is recommended in the protected cultivation of *B. schreberi* which had better performance than white LED light source.

**Declarations**

**Author contribution statement**

Changfang Zhou: Conceived and designed the experiments; Wrote the paper.

Jiafeng Li: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Cuiyu Yi, Chenrong Zhang, Fan Pan, Chun Xie: Performed the experiments.

Wenzong Zhou: Analyzed and interpreted the data; Wrote the paper.

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**Data availability statement**

Data included in article.

**Declaration of interests statement**

The authors declare no conflict of interest.

**Additional information**

No additional information is available for this paper.

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