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Effect of different LED-lighting quality conditions on growth and photosynthetic characteristics of saffron plants (*Crocus sativus* L.)

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Abstract

The effects of different light-emitting diode (LED) lights on saffron growth and photosynthetic characteristic were explored. Physiological mechanisms were explained by chlorophyll *a* fluorescence transient curves (OJIP) and JIP-test parameters. A decrease in the red to blue light ratio resulted in negative effects, particularly for monochromatic blue (B) LED light; saffron seedlings showed reduced chlorophyll accumulation, inhibited leaf elongation, and decreased photosynthetic performance. In the OJIP curve, the higher positive K-band observed for B LED light indicated that oxygen-evolving complex activation significantly decreased. B LED light inhibited the electron transport between primary quinone acceptor and secondary quinone acceptor as well as the existence of reducing plastoquinone centers, and increased energy dissipation of reaction centers. Otherwise, the red to blue light ratio of 2:1 had a positive effect on saffron cultivation, resulting in the longest leaf lengths, highest chlorophyll content, and photosynthetic characteristics. This study provides theoretical guidance for saffron agricultural practices.

Keywords: chlorophyll fluorescence; LED light; photosynthesis; saffron.

Introduction

Light is one of the most critical environmental factors for plant growth and development. The quality of light (spectral quality), such as LED (light-emitting diode) light, has a profound influence on the morphogenesis and photosynthesis of plants (Xu *et al.* 2020). LED lights are widely applied to a variety of plants in agriculture owing to their advantages of lower heat generation, easier control, and higher energy efficiency for irradiation

Highlights

- Blue light has negative effects on saffron leaf growth and photosynthetic performance
- Blue light reduced PSII oxygen-evolving complex activation
- R2B1 LED light is suitable for saffron cultivation

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Abbreviations: B – blue light; C_i – intercellular CO_2 concentration; DI_0/RC – dissipated energy flux per reaction center; E – transpiration rate; ET_0/RC – electron transport flux from Q_A to Q_B; F_m – the maximum fluorescence in the OJIP curve; F_o – the minimum fluorescence in the OJIP curve; g_s – stomatal conductance; M_0 – the initial slope from 0.02 ms to 300 ms in a linear time scale; OEC – oxygen-evolving complex; PI_{total} – performance index for the conservation of energy from photons absorbed by the PSII antenna to the reduction of PSI acceptors; P_N – net photosynthetic rate; PQ – plastoquinone; Q_A – primary quinone acceptor of PSII; Q_A^- – reduced primary quinone acceptor of PSII; Q_A^+ – oxidized primary quinone acceptor of PSII; Q_B – secondary quinone acceptor of PSII; R – red light; RC – reaction center; RC/CS_m – reaction centers per CS (t = m); V_I – normalized variable fluorescence at 30 ms (I point); V_J – normalized variable fluorescence at 2 ms (J point); VPD – vapor pressure deficit; V_t – normalized variable fluorescence at time t; WUE – water-use efficiency; δ_{Ro} – efficiency with which an electron from Q_B is transferred until PSI acceptors; φ_{Eo} – quantum yield of the electron transport flux from Q_A to Q_B; φ_{Po} – maximum quantum yield of primary photochemistry; φ_{Ro} – quantum yield of the electron transport flux until the PSI electron acceptors; ψ_{Eo} – electron transport efficiency from Q_A^- to the PSI electron end acceptors; ψ_{Ro} – electron transport efficiency except Q_A.

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(Li *et al.* 2020). However, LED illumination has different effects on growth, photosynthesis, and metabolism because different plants adjust their biochemistry and fix CO_2 differently (Paradiso *et al.* 2022). The P_N (net photosynthetic rate), root elongation, and the relative expression of genes, such as *rbcS* and *psbA*, were promoted under monochromatic red (R) light, while blue (B) light reduced the plant height of tomato (*Solanum lycopersicum*) (Wu *et al.* 2014). Moreover, soybean (*Glycine max*) and eggplant (*S. melongena*) grown with 100% R (monochromatic red light) had the highest contents of chlorophyll (Chl) *b* and total Chl. However, they retained the lowest Chl fluorescence parameters (Di *et al.* 2021, Fang *et al.* 2021). Otherwise, plants grown in mixtures of B- and R-light environments manifested an improvement in seedling growth and development by enhancing the synthesis of photosynthetic pigments, conversion of energy, and utilization efficiency of PSII, and thus, delayed leaf senescence (Wang *et al.* 2017).

As discussed above, the response of plants under different LED lights varied. This is owing to major differences in the response of the plant photoprotection and photoinhibition mechanisms. Excess light is a comprehensive indicator of the environment that is absorbed by the light-harvesting system of photosynthetic organisms, and it communicates the presence of intense light or any unfavorable environmental conditions for growth and photosynthesis (Demmig-Adams *et al.* 2006). The visible stress symptoms inhibit germination, stunt growth, and cause leaf chlorosis. In detail, unfavorable conditions can result in similar or identical photosynthetic disturbances, including the capture for pigments and light, transport of photosynthetic electrons, CO_2 effects, and stomatal conductance at different structure–function levels (Paunov *et al.* 2018). The induction of fluorescence in Chl *a* can probe the plant photosynthetic process and provides more detailed information about the electron transfer process in PSII and beyond (Chen *et al.* 2016, Khan *et al.* 2021).

Saffron (*Crocus sativus* L.) is a triploid plant that flowers in the autumn and grows in the winter and spring. Its flower has three stigmas that benefit health by activating blood, resolving stasis, preventing tumors and cancer, remediating cardiovascular diseases, enhancing the production and activity of antioxidant enzymes in diabetes mellitus, and relieving menstrual symptoms (Chinese Botany Editorial Board 1985, Samarghandian and Borji 2014, Liu *et al.* 2016, Jazani *et al.* 2022). The global functional food and dietary supplement markets are growing quickly and the demand for high-quality herbs, including saffron, is increasing (Sendker and Sheridan 2017). There is an enormous market demand for saffron stigmas, which are widely utilized for health tea, pharmaceuticals, and precious spices. The saffron stigmas are referred to as 'red gold' worldwide since they are the most expensive spice (Kothari *et al.* 2021). However, the cultivation of saffron has been limited owing to the low yield of flowers, which are affected by the environmental conditions during growth (Gresta *et al.* 2008). Many studies intensively report methods how to stimulate the growth of saffron, eliminate water stress, control water salinity during irrigation, apply manure, control temperature and light (Renau-Morata *et al.* 2012, Yarami and Sepaskhah 2015, Zhou *et al.* 2022). Previous studies lack sufficient and detailed information that describes the effects of LED light on saffron growth and photosynthetic characteristics. There are no reports in the literature about further exploring the critical physiological factors for the differences by analysis of the trapping of pigments and light, transport of photosynthetic electrons, absorption of light, and dissipation in reaction centers at different structure and function levels.

We aimed to evaluate the effects of LED supplementation on the growth and photosynthesis of saffron with the consideration of LED advantages. We further provide an in-depth explanation of the significant factors for the difference of saffron in growth and photosynthetic characteristics under different light qualities by analyzing the trapping of pigments and light, transport of the photosynthetic electrons, absorption of light and dissipation of the reaction center. This study brings new insights to explore the critical physiological factors of the morphological differences of saffron leaves irradiated by LED light, to determine the best proportion of LED light for saffron growth, and to provide theoretical guidance to improve the agricultural cultivation of saffron.

Materials and methods

Plant materials and growth conditions: Mother corms from the Baihe Seedlings Base of Shanghai Academy of Agricultural Sciences (Shanghai, China), of a mass between 20–25 g, were selected for the experiment. Thirty corms were planted at the end of the flowering period in a plastic crate (60 × 40 × 180 cm) with a culture substrate. The culture substrate was a 1:2 (v/v) mixture of perlite (4–8 mm diameter) and peat (20–40 mm fiber), added to a total of 36 crates used in the experiment. All crates with saffron plants were placed in the plant factory after one week. The day and night temperatures in the plant factory were between 8–15°C, which is suitable for saffron growth. All the saffron plants were subjected to the irradiance of 250 ± 50 μmol(photon) m^{-2} s^{-1} (8/16-h day/night) provided by six LED lights, and the relative humidity was maintained at 60–70%. The N-P-K proportion of fast water-soluble fertilizers applied by drift irrigation was 30-10-10, with a 1.25 ml min^{-1} drift irrigation speed, and the machine was utilized once for 1 min daily.

Light treatments: The experiments were performed with a completely random design of six different light combinations to study the effect of LEDs (*T10*, 18 W; *Aisheng Biotechnology Technology Co., Ltd.*, China) on saffron growth, and white LED light was used as the control. The corms irradiated by LED lights in the experiment are shown in Fig. 1: CK (control, 100% white light), B (100% blue light), R (100% red light), R1B2 (a 1:2 proportion of red to blue light), R1B1 (a 1:1 proportion of red to blue light), and R2B1 (a 2:1 proportion of red to blue light). The light spectra (Fig. 1S, *supplement*)

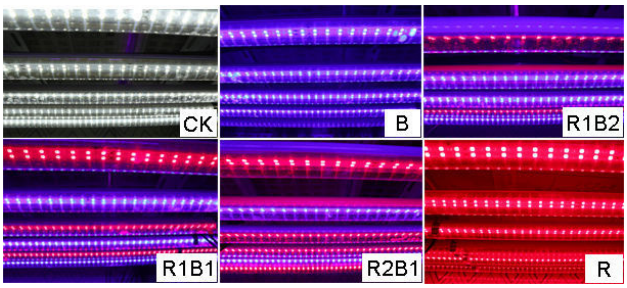

Fig. 1. The LED light conditions in the experiment. B – monochrome blue light; CK – white light; R – monochrome red light; R1B2 – red to blue light ratio of 1:2; R1B1 – red to blue light ratio of 1:1; R2B1 – red to blue light ratio of 2:1.

were analyzed on corms in the plates using a portable spectrometer (*ALP-01*, *Ushio*, *Asensetek*, Cypress, CA, USA). The peak wavelengths of the blue and red LED were 450 and 660 nm, respectively. The PPFD from the LED light in all the treatments was set at 250 ± 50 μmol m^{-2} s^{-1}. The experiment was started on 11 November 2020 and terminated on 30 May 2021. The corms were grown within the growth factory under 8-h photoperiod for 141 d.

Saffron growth and photosynthesis: The length of saffron leaves from the apex to the base grown under different LED lights was measured using a steel ruler (0.1 cm) at 120 d. Total Chl content was measured at the middle part of functional saffron leaves using a portable chlorophyll meter *SPAD-502 PLUS* (*Konica Minolta Optics*, Tokyo, Japan). Nine individual plants were measured for each treatment at 120 d.

A *CIRAS-3* portable photosynthesis system (*PP Systems*, Amesbury, MA, USA) was used to measure the photosynthetic parameters, including the net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), intercellular CO_2 concentration (C_i), water-use efficiency (WUE), and vapor pressure deficit (VPD) at 15°C, PPFD of 260 μmol m^{-2} s^{-1}, 60–70% relative humidity, and ambient CO_2 (390 ppm) between 8:00 and 11:00 h at 120 d. Nine individual plants were measured for each treatment.

Chl fluorescence rise kinetics and JIP-test parameters: Chl fluorescence was measured using a *Handy PEA* continuous excitation fluorimeter (*Handy Plant Efficiency Analyzer*, *Hansatech Instruments*, *Ltd.*, King's Lynn, UK). The Chl fluorescence data of saffron leaves under different LED lights were measured after 20 min of dark adaption. The induction curves of Chl *a* were recorded for 1 s with PPFD of 3,000 μmol m^{-2} s^{-1}. The special points (fluorescence at a time) in the OJIP curve were O (0.02 ms), L (0.15 ms), K (0.3 ms), J (2 ms), I (30 ms), and P (300 ms). Nine individual plants were measured for each treatment at 120 d.

To illustrate the dynamic process of the electron transport chain, the relative fluorescence parameters were calculated by double normalization of the moment Chl fluorescence values to the endpoint within different intervals with the OJIP part of the transient: OP, OK, OJ, and OI. F_o was the minimum fluorescence in the OJIP curve, F_m was the maximum fluorescence in the OJIP curve, and V_t was normalized variable fluorescence at time t in the OJIP curve. The formulas were as follows: $V_t = (F_t - F_o)/(F_m - F_o)$; $W_{OK} = (F_t - F_o)/(F_K - F_o)$; $W_{OJ} = (F_t - F_o)/(F_J - F_o)$; $W_{OI} = (F_t - F_o)/(F_I - F_o)$; $W_L = (F_L - F_o)/(F_K - F_o)$; $\Delta W_L = W_{L(treatment)} - W_{L(control)}$; $W_K = (F_K - F_o)/(F_J - F_o)$; $\Delta W_K = W_{K(treatment)} - W_{K(control)}$; $V_J = (F_J - F_o)/(F_m - F_o)$; $\Delta V_J = V_{J(treatment)} - V_{J(control)}$; $V_I = (F_I - F_o)/(F_m - F_o)$; OEC centers = $[1 - (V_K/V_J)]_{(treatment)}/[1 - (V_K/V_J)]_{(control)}$, $M_0 = 4(F_{300\mu s} - F_o)/(F_m - F_o)$ to clarify the structure and function of the photosynthetic apparatus by describing the primary photosynthetic reactions in PSII. The JIP-test parameters included DI_0/RC (dissipated energy flux per reaction center), ET_0/RC (electron transport flux from Q_A to Q_B), PI_{total} (performance index for the conservation of energy from photons absorbed by the PSII antenna to the reduction of PSI acceptors), φ_{Eo} (quantum yield of the electron transport flux from Q_A to Q_B), φ_{Po} (maximum quantum yield of primary photochemistry), φ_{Ro} (quantum yield of the electron transport flux until the PSI electron acceptors), δ_{Ro} (efficiency with which an electron from Q_B is transferred until PSI acceptors), ψ_{Ro} (electron transport efficiency except Q_A), ψ_{Eo} (electron transport efficiency from Q_A^- to the PSI electron end acceptors), RC/CS_m (reaction centers per CS), which were measured at 120 d.

Statistical analysis: A statistical analysis was performed using *SPSS 19.0* (*IBM*, *Inc.*, Armonk, NY, USA). The growth and physiological parameters were performed using a one-way analysis of variance (*ANOVA*) (P<0.05) and *Duncan*'s test (P<0.05). The data were processed and graphed using *Microsoft Excel 2007* (Redmond, CA, USA) and *Origin Pro Version 8.5E* (*OriginLab*, Northampton, MA, USA).

Results

Effects of different LED lights on the growth: Saffron plants exposed to varying LED lights exhibited several morphological differences after 120 d. The saffron seedlings, exposed to B and R1B2 light, were visibly stressed and displayed symptoms of senescence, which were evident due to the appearance of yellow leaves in the seedlings and short leaves. The seedlings of the CK, R2B1, and R treatments had slightly yellow tips on their leaves (Fig. 2*A*). Otherwise, treatment with B resulted in leaves, which were 45.2 cm long, while those treated with R1B2 were 46.4 cm long. Conversely, the saffron leaves irradiated by R were 51.8 cm long, and those of R2B1 were 52.6 cm long, indicating significant enhancement by 8.8% and 10.5% compared with the CK, respectively, while the plants treated with R1B1 were less affected (Fig. 2*B*).

The content of total Chl decreased > 50% owing to light irradiation with B and R1B2 (52.9 and 59.5%, respectively). The R and R2B1 strongly contributed to the

accumulation of Chl in the saffron leaves. The SPAD value was 29.6 in the R treatment and 29.1 in the R2B1 treatment, resulting in an increase of 18.7 and 16.5% compared with the CK, respectively. Irradiation with B light resulted in stress and stronger inhibition of the length of leaves, whereas exposure to R light stimulated the saffron leaves to grow longer and become greener at 120 d (Fig. 2*B*).

Photosynthetic characteristics: The photosynthetic characteristics of the saffron leaves treated with different LED lights are shown in Fig. 3. The values of P_N, E, and g_s were the highest under R2B1 light at 16.69 μmol m^{-2} s^{-1}, 3.92 mmol m^{-2} s^{-1}, and 1,404.5 mmol m^{-2} s^{-1}, respectively, which were 69.6, 113.0, and 323.2% higher than those under the white LED light (control), respectively

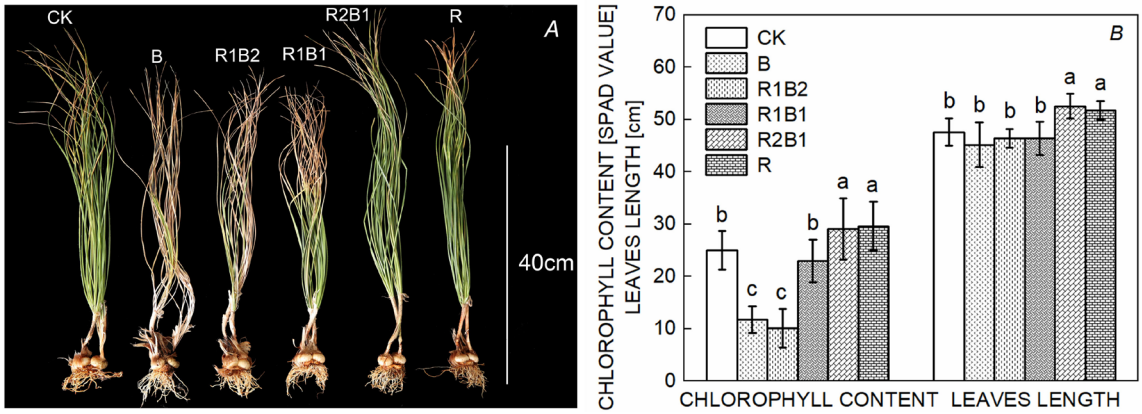

Fig. 2. (*A*) The difference in morphology of saffron plant grown in plant factory at 120 d. (*B*) The leaf lengths and chlorophyll content of saffron with different LED lights. *Different letters* indicate significant differences in treatments (P<0.05).

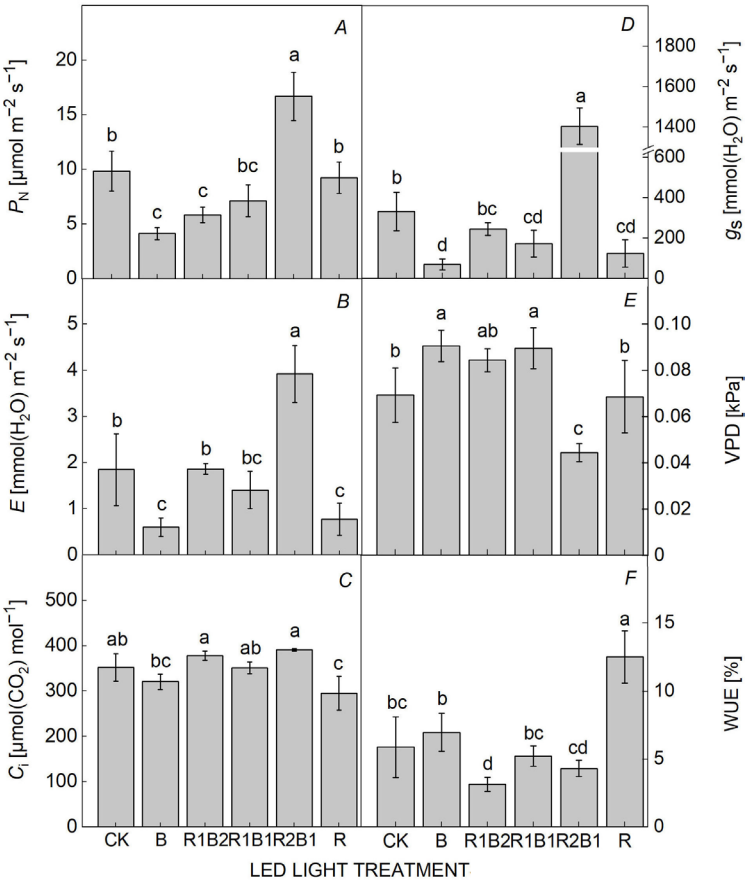

Fig. 3. Effects of different types of LED lights on the photosynthetic characteristics of saffron leaves. (*A*) Net photosynthetic rate (P_N); (*B*) transpiration rate (E); (*C*) intercellular CO_2 concentration (C_i); (*D*) stomatal conductance (g_s); (*E*) vapor pressure deficit (VPD); (*F*) water-use efficiency (WUE). Values are the means ± SD (n = 9). *Different letters* indicate significant differences in treatments (P<0.05).

(Fig. 3*A*,*B*,*D*). However, the P_N decreased as the proportion of blue light increased with different LED lights except for R light. In detail, there was maximum P_N in the R2B1 treatment, which was also higher than that of the R treatment. The lowest levels of P_N, g_s, and E were observed in the B light treatment, *i.e.*, 4.13 μmol m^{-2} s^{-1}, 69.96 mmol m^{-2} s^{-1}, and 0.61 mmol m^{-2} s^{-1}, respectively. In detail, B-irradiated saffron seedlings were inhibited by approximately 58.0, 66.8, and 78.9%, respectively, compared with the CK, whereas there was no clear difference in the C_i (intercellular CO_2 concentration) with the CK (Fig. 3*A–D*).

The minimum C_i and maximum WUE (water-use efficiency) were apparent in the R treatment (295.21 μmol mol^{-1} and 12.5%, respectively). The C_i and WUE under the R light decreased by 16.2% and increased by 114.1% compared with the CK, respectively (Fig. 3*C*,*F*). Moreover, the VPD (vapor pressure deficit) of leaves was more pronounced under the blue light treatments, and the red lights were more effective at promoting WUE and decreasing the VPD. Among those different LED lights, the lowest VPD was observed in the R2B1 treatment, and its VPD value was 0.044 kPa (Fig. 3*E*).

Raw fluorescence rise kinetics in OJIP curves: The fluorescence rise kinetics of the OJIP curves of the saffron leaves treated with B, R1B2, R1B1, R2B1, R, and white LED light gradually increased and reached the maximum fluorescence value equal to F_m (maximum fluorescence in the OJIP curve) at the P-step (300 ms) (Fig. 4*A*). The R2B1-treated leaves were higher than that of the control or other light treatments in all phases of the OJIP curve (Fig. 4*A*). Moreover, an increase in the F_o (minimum fluorescence in OJIP curve) and F_m values was observed when the plants were treated with R2B1; values were remarkably higher than those of the CK by 22.7 and 9.0%, respectively (Fig. 4*B*).

In the OJIP curve, in the case of the R1B2, R1B1, and R light treatments, the fluorescence level in the phase from the O-step (0.02 ms) to the K-step (0.3 ms) was highly similar to the control. Conversely, the levels of fluorescence in the phase from the K-step to P-step (300 ms) decreased compared with the control (Fig. 4*A*). The values of F_m in the R1B1, R, and R1B2 treatments were lower by 13.3, 19.6, and 28.3% than those under CK, respectively (Fig. 4*B*).

Moreover, by increasing the time of irradiance on saffron seedlings from 0.3 to 1,000 ms, the fluorescence induction kinetics plateaued in the B light treatment, which completely lost the O–J–I–P polyphasic transient (Fig. 4*A*). However, a significant decrease in F_o and F_m were observed in the B treatment, and the values of F_o and F_m decreased by 35.5 and 56.7% relative to the control, respectively (Fig. 4*B*).

The relative variable fluorescence V_t: To further analyze the differences in the shape of induction curves under different light treatments, the transients of the double normalized fluorescent signal (V_t and ΔV_t) at a logarithmic time scale are shown in Fig. 5*A*,*B*. In the O-step to K-step period, steeper initial increases were observed in the B and R1B2 light treatments, and the M_0 (initial slope, $R^2 \geq 0.94$) values of the B and R1B2 treatments increased by 78.1 and 56.9%, respectively (Fig. 5*A*,*C*). Moreover, the B and R1B2 light treatments also led to a significant rise in the J-step (Fig. 5*A*), and the V_J (normalized variable fluorescence at 2 ms in J point) value in the B light increased significantly by 36.7% (the V_J value was 0.68 in B treatment) compared with the CK. Moreover, there were positive peaks in F_o–F_J, and the values of ΔV_J (double normalized variable fluorescence in J point) in the B, R1B2, R1B1, and R light treatments were significantly higher than those in the CK, particularly in the B light (Fig. 5*B*,*D*). Otherwise, the LED lights resulted

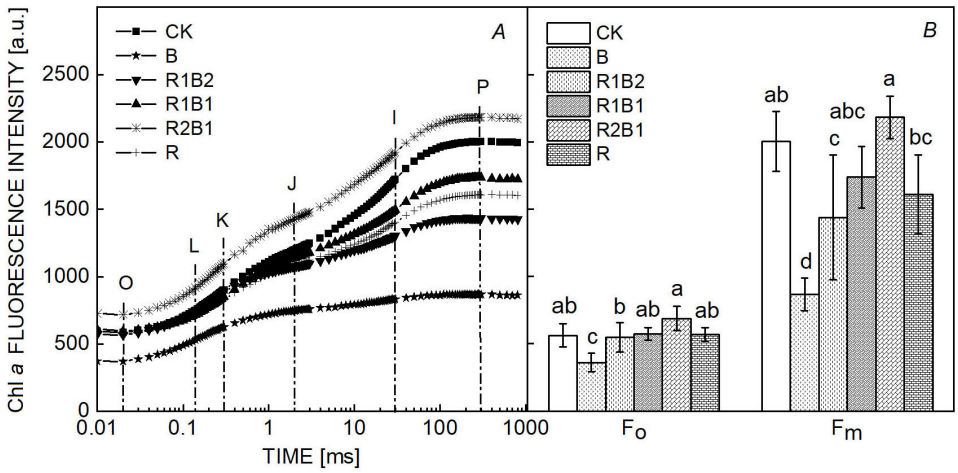

Fig. 4. (*A*) Raw Chl *a* fluorescence rise kinetics of saffron seedlings treated by different LED lights on a logarithmic scale. (*B*) Effects of different LED lights on the F_o (minimum fluorescence in the OJIP curve), F_m (maximum fluorescence in the OJIP curve), and F_v (maximal variable fluorescence) values. Values are the means ± SD (n = 9). *Different letters* indicate significant differences in treatments (P<0.05).

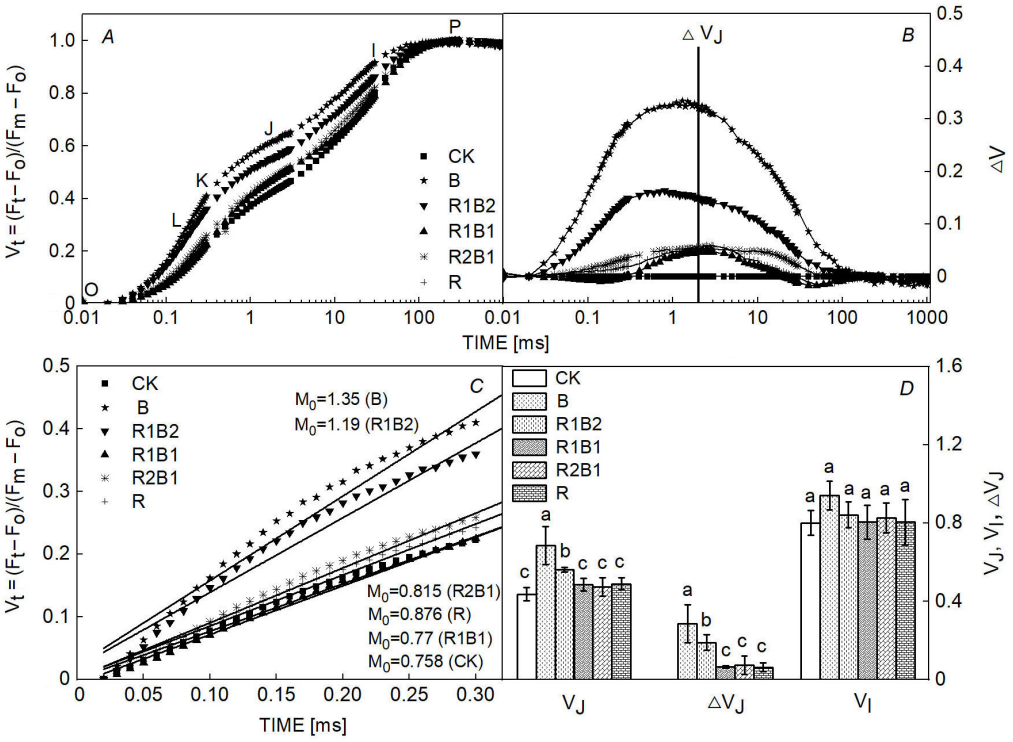

Fig. 5. Effects of different LED lights on relative fluorescence. (*A*) Chl *a* fluorescence rise kinetics normalized by F_o and F_m as $V_t = (F_t - F_o)/(F_m - F_o)$ in a logarithmic time scale. (*B*) $\Delta V_t = V_{t(treatment)} - V_{t(control)}$. (*C*) The relative variable fluorescence V_t. M_0 was the time from 0.02 ms to 300 ms in a linear time scale to show the initial slope. (*D*) The values of V_J (normalized variable fluorescence at 2 ms in J-point), ΔV_J (double normalized variable fluorescence in J-point), and V_I (normalized variable fluorescence at 30 ms in I-point) under six different LED light treatments. Values are the means ± SD (n = 9). *Different letters* indicate significant differences in treatments (P<0.05).

in the increase of normalized fluorescent curve at the I-step (Fig. 5*A*). Nevertheless, the V_I (normalized variable fluorescence at 30 ms in I point) values of LED lights did not differ significantly from the CK marginal means, and the ranges were all between 0.80 and 0.94 (Fig. 5*B*).

The O–K and O–J phase: To further evaluate the processes reflected in the O–K and O–J phase, the double normalization of the moment Chl fluorescence curves is shown in Fig. 6. The L-band shown in Fig. 6*A*, which was double normalized by the O- (20 μs) and K-step (300 μs) for different LED treatments, indicated the polymerism between different components of PSII or energy transfer connectivity between the antenna pigments and active reaction center (RCs) of PSII. It indicated that the B and R1B2 treatments slightly increased the L-band and were not significantly different from the other LED light treatments (Fig. 6*A*).

To understand the effect of LED lights on the O–J phase, the K-band appeared in Fig. 6*B* and represented the fluorescence rise kinetics curve with double normalization by the O-step (20 μs) and J-step (2 ms). The K-band is known as an indicator of the inactivation of the oxygen-evolving complex (OEC) at the donor PSII side (Strasser *et al.* 2004). It was shown that the LED light of B and R1B2 had the strongest effect on the K-band. Moreover, W_K significantly increased by 31.6 and 23.6%, respectively, in the K-band compared with that of the CK (Fig. 6*B*,*D*). It was also observed that the B and R1B2 treatments increased significantly in the O–J phase, and the ΔW_K values were 0.169 and 0.139, respectively, which were significantly higher than those of the CK. However, there were no obvious differences in the CK under R1B1, R2B1, and R light treatments. In contrast, the OEC active values (Fig. 6*C*) decreased significantly by treatment with the B light, and the OEC minimum was 0.476, which decreased by 110% compared with that of the CK. Otherwise, the F_K/F_J value significantly increased in the B treatment by 16% compared with that of the CK. This analysis revealed that the B light damaged the fraction of active OEC centers.

The O–I phase: The amplitude of the W_{OI} curve involves the pool size of the end electron acceptors on the PSI acceptor side (Oukarroum *et al.* 2009). The amplitude of W_{OI} curves was greater, indicating a stronger positive effect on the pool size. The R2B1, CK, and R light treatments had larger amplitudes in different LED lights. The part of the W_{OI} curve in the I-step to P-step ($W_{OI} \geq 1$) in the B treatment decreased the most among six different LED lights (Fig. 7*A*). The smallest pool size of the end electron acceptors in the PSI acceptor side occurred

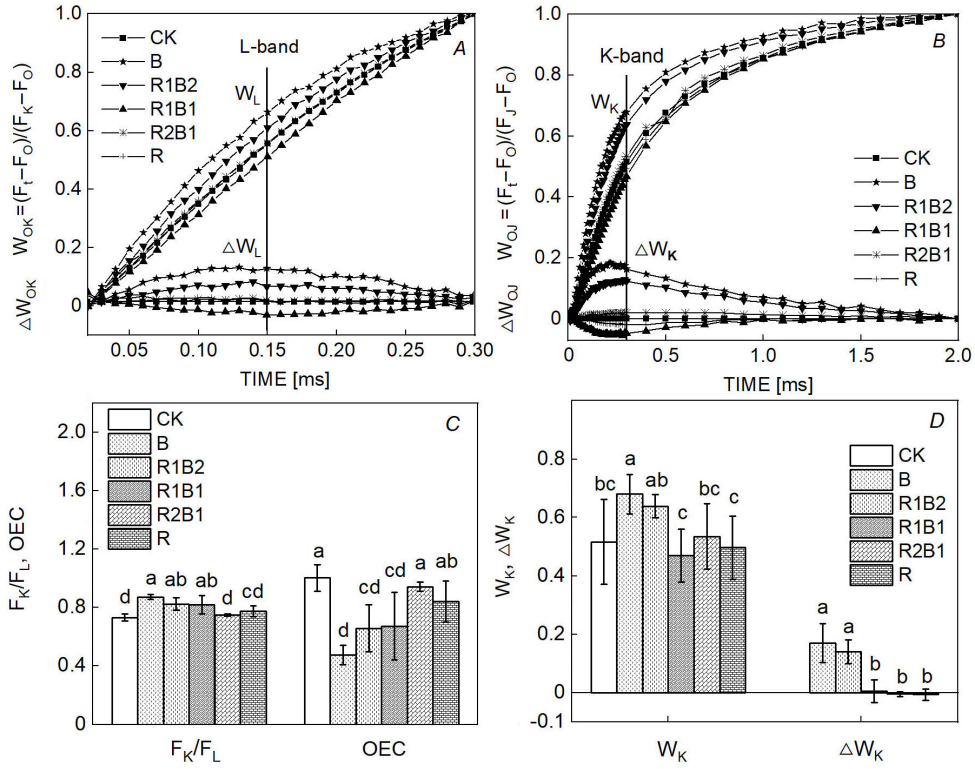

Fig. 6. The effects of different LED lights on double normalization fluorescence curves. (*A*) $W_{OK} = (F_t - F_o)/(F_K - F_o)$: the normalized fluorescence rise kinetics curves by O- (0.02 ms) and K-step (0.3 ms) of the different LED treatments, $\Delta W_{OK} = W_{OK(treatment)} - W_{OK(control)}$: the double normalized fluorescence rise kinetics curves by O- (0.02 ms) and K-step (0.3 ms) of the different LED treatments. (*B*) $W_{OJ} = (F_t - F_o)/(F_J - F_o)$: the normalized fluorescence rise kinetics curves by O- (0.02 ms) and J-step (2 ms) of the different LED treatments, $\Delta W_{OJ} = W_{OJ(treatment)} - W_{OJ(control)}$: the double normalized fluorescence rise kinetics curves by O- (0.02 ms) and J-step (2 ms) of the different LED treatments. (*C*) F_K/F_J: ratio of fluorescence intensity at the K-step of OJIP to fluorescence intensity at the J-step of OJIP; OEC (oxygen-evolving complex) centers = $[1 - (V_K/V_J)]_{(treatment)}/[1 - (V_K/V_J)]_{(control)}$. (*D*) $W_K = (F_K - F_o)/(F_J - F_o)$; $\Delta W_K = W_{K(treatment)} - W_{K(control)}$. *Different letters* indicate significant differences in treatments (P<0.05).

following treatment with the B light, and the values under the B treatment were significantly smaller than those of the control or others, and the part of PSI was damaged (Fig. 7*B*).

JIP-test parameters: To further assess the effect of LED light on photosynthesis, several JIP-test parameters are shown in Fig. 8; they quantify the conformation, structure, and function of the photosynthetic apparatus. Under different LED lights, the lowest value of quantum yield parameters were all shown in the B treatment, and the PI_{abs}, φ_{Po}, φ_{Eo}, and φ_{Ro} of the quantum yields decreased by 88.7, 30.1, 67.4, and 70.4%, respectively, compared with those of the CK (Fig. 8). The flux ratios of ψ_{Ro}, ψ_{Eo}, and δ_{Ro} decreased in the B light, and the lowest efficiencies of ψ_{Ro}, ψ_{Eo}, δ_{Ro} were observed in the B treatment. However, the maximum δ_{Ro} and ψ_{Ro} were all observed in the R2B1 light, which indicated a high electron efficiency from the photosystem electron transport chain to the end electron acceptors on the PSI acceptor side. The energy flux in the PSII reaction center ET_0/RC showed the minimum in B light, which decreased by 40.6% compared with that of the CK. Conversely, the maximal ET_0/RC appeared in the R1B1 treatment, which increased by 2.3% compared with that of the CK. Otherwise, the energy dissipation per PSII reaction center DI_0/RC was reduced the most significantly in the B treatment. Conversely, the energy dissipation per reaction center was significantly the lowest in the B treatment. The B and R1B2 treatments of RC/CS_m decreased significantly by 74.0 and 47.1%, respectively, compared with that of the CK.

Discussion

Red LEDs have been shown to have a highly significant role in improving plant growth. Previous research has shown that the fresh and dry mass, leaf area and number, plant height, flower number, and diameter of *Hypericum perforatum* L. were significantly highest when the R/B ratio was enhanced (Karimi *et al.* 2022). Additionally, the results of various studies have shown that highbush blueberry (*Vaccinium corymbosum*) (Hung *et al.* 2016), soybean (*Glycine max*) (Fang *et al.* 2021), lettuce (*Lactuca sativa*) (Hoenecke *et al.* 1992, Shimizu *et al.* 2011) and other dicotyledonous plants (Sabzalian *et al.* 2014, Cioć *et al.* 2018) grown under a high-proportion of red-

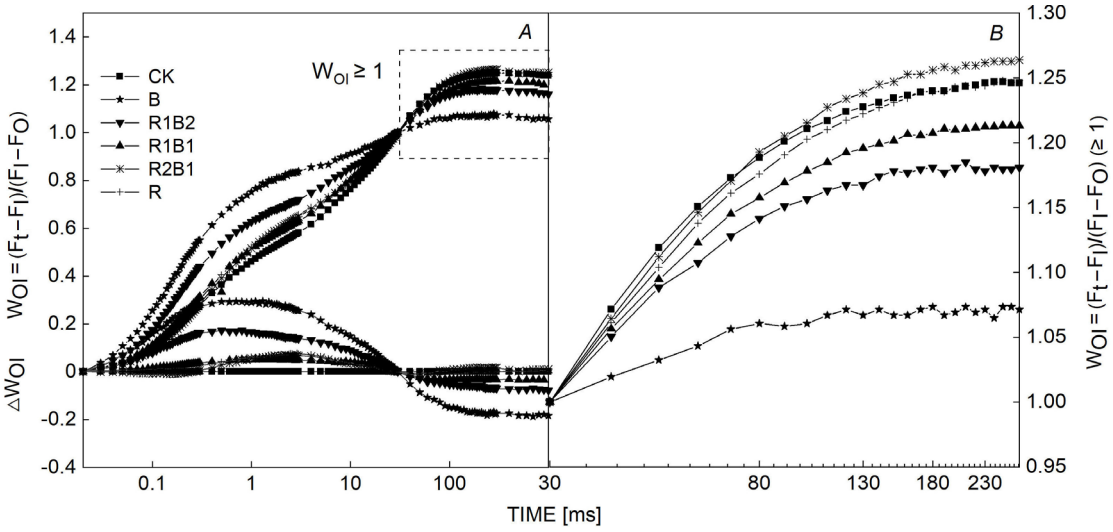

Fig. 7. (*A*) $W_{OI} = (F_t - F_o)/(F_I - F_o)$: the normalized fluorescence rise kinetics curves by O- (20 ms) and I-step (300 ms) of different LED treatments, $\Delta W_{OI} = W_{OI(treatment)} - W_{OI(control)}$: the double normalized fluorescence rise kinetics curves by O- (20 ms) and I-step (300 ms) of different LED treatments. (*B*) The W_{OI} curves from 30 to 270 ms.

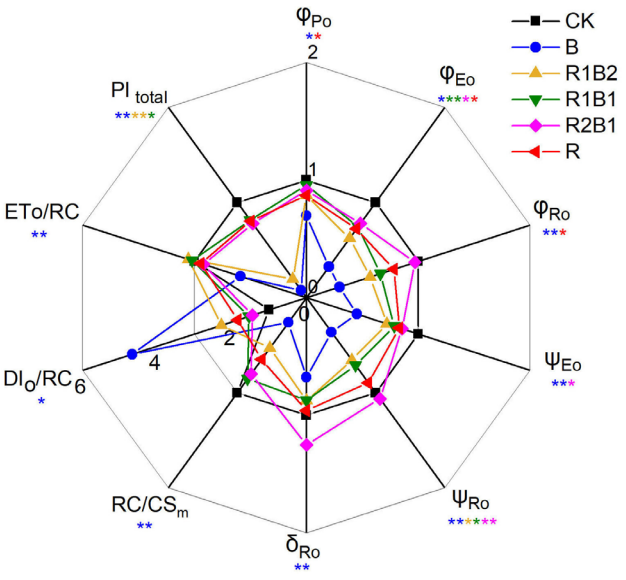

Fig. 8. The spider plots of the chlorophyll fluorescence parameters of saffron leaves under different LED lights relative to CK. DI_0/RC – dissipated energy flux per PSII; ET_0/RC – electron transport flux from Q_A to Q_B; PI_{total} – performance index for the conservation of energy from photons absorbed by the PSII antenna to the reduction of PSI acceptors; φ_{Eo} – quantum yield of the electron transport flux from Q_A to Q_B; φ_{Po} – maximum quantum yield of primary PSII photochemistry; φ_{Ro} – quantum yield of the electron transport flux until the PSI electron acceptors; δ_{Ro} – efficiency with which an electron from Q_B is transferred until PSI acceptors; ψ_{Ro} – electron transport efficiency except for Q_A; ψ_{Eo} – electron transport efficiency from Q_A^- to the PSI electron end acceptors; RC/CS_m – reaction centers per CS (t = m). * significant differences with the CK (P<0.05), and ** significant differences with the CK (P<0.01).

emitting light develop higher shoots and leaves, as well as greater Chl content. Our results showed that LED lights with a high proportion of red light promoted the growth of saffron seedling leaves, and the R2B1 treatment had the longest leaf length and a higher content of Chl in the saffron leaves. The wavelengths of red light fit perfectly with the absorption peak of chlorophylls which would be the most efficient light (Hoenecke *et al.* 1992, Dou *et al.* 2017). In contrast, blue light inhibited cell growth and stem elongation, owing to its regulation by blue light photoreceptors and changes in gene expression (Lin 2000).

Photosynthesis is an important and necessary process for plant growth and development, which converts light energy into chemical energy by absorbing light and providing energy for plant growth (Yeh and Chung 2009). Typically, it is known that photosynthesis reduction can be caused by a stomatal limitation or nonstomatal limitation. Our results indicated that P_N, E, and g_s significantly decreased in the B and R1B2 treatments compared with the CK, while C_i remained similar to the control, which indicated that the key point of saffron photosynthetic inhibition by LED light irradiation was the nonstomatal limitation. Previous studies concluded photosynthetic carotenoids have absorption maxima for blue wavelengths and differ in their efficiency (35 to 90%) for the transfer of excitation energy to chlorophyll, depending on the type of carotenoid and its position within the photosynthetic apparatus. In addition, Hogewoning *et al.* (2012) showed that a slight reduction in the amount of LHCII was observed in the leaves grown under blue light. In our study, saffron did not efficiently use blue light which resulted in low photosynthesis.

However, the R2B1 treatment significantly stimulated the increase of P_N, E, and g_s, improved the WUE of plants, and reduced the water deficiency during the late

growth stage of saffron. Previous studies demonstrated that red light resulted in a higher maximum quantum yield, photosynthetic rate, and electron transport rate compared to blue light (McCree 1971, Liu and van Iersel 2021). In our study, a higher proportion of red light in the LED lights produced higher chlorophyll contents, P_N, and maximum quantum yield in leaves. Red light contributes to higher effective photosynthetic efficiency and chlorophyll content in saffron plants. However, the P_N increased as the proportion of blue light decreased with different LED lights except for the R LED light in our study. In detail, the R treatment had lower P_N values compared with the maximum P_N of R2B1 light. Miao *et al.* (2019) explained the phenomenon that monochromatic red light easily induces red light syndrome by long-term irradiation, whereas the decreased P_N of the red light syndrome was effectively alleviated by adding blue light to monochromatic red light.

To explore how different LED lights affected PSII and localized their initial action sites on PSII, we evaluated the processes of the OJIP curve under different LED lights. During the initial period of the complete oxidation of the Q_A receptor (plastoquinone) (Q_A^+), the excited chlorophyll molecules in the PSII antenna emit fluorescence. A significant decrease in F_o and F_m was observed when the plants were treated by B, which manifested as a smooth straight line in the kinetics of original Chl *a* fluorescence. The decreases in F_v with time in the kinetics of original Chl *a* fluorescence were attributed to stress that reduced the amount of chlorophyll in the leaf tissues, increased the dissipation of nonradiative energy (DI_0/RC), and rendered the PSII reaction center inactive (Jefferies 1992, Hong *et al.* 1999, Tsai *et al.* 2019). Thereby B-treated leaves had the lowest Chl content and earliest leaf senescence and completely lost the O–J–I–P polyphasic transient compared with leaves treated with the other LED lights, which suggests that the plants could be stressed at 120 d during this growth stage.

To fully understand the physiological factors of photosynthetic differences in saffron leaves under different light qualities, Chl *a* fluorescence rise kinetics under different LED lights were systematically analyzed. M_0 indicated the maximum reduction rate of Q_A in the initial stage; the reduced Q_A molecule can be reoxidized by electron carriers outside Q_A in the electron transport chain during the later stage (Strasser *et al.* 1995). Previous studies reported that M_0 under salt or high-temperature stress increased significantly in the OJIP curve, demonstrating that electrons transferred from Q_A to Q_B on the PSII acceptor side were blocked (Jiang *et al.* 2020, Zha *et al.* 2021). In the O–K phase, the curve increased rapidly with a higher straight slope (M_0) under the B and R1B2 treatments in this study, which indicated saffron plant suffered from B LED stress and the electrons transferred from Q_A to Q_B on the PSII acceptor side were blocked, conversely Q_A was in high-speed supplementation.

There was an increase in the K-step with the B and R1B2 treatments, which could be an indirect effect of reactive oxygen species and the results of electron leakage caused by the inhibition of PSII electron flow beyond Q_A (Strasser *et al.* 2000, 2004). The K-step is widely used to indicate the status of the active OEC centers at the PSII donor side, which is specifically attributed to the OEC destruction by the release of the manganese cluster (Strasser *et al.* 2004, Chen *et al.* 2016). Previous studies reported that high temperature and drought stress would result in K-step rising and OEC destruction in grape, cherry, and weed, respectively (Chen *et al.* 2016, Mihalhević *et al.* 2021, Zha *et al.* 2021). In this study, the W_K and F_K/F_J increased significantly and reached the highest values under the B treatment, thus resulting in the lowest activation of the OEC compared to other treatments. We found that in this study blue light resulted in K-step rising and OEC inactivation, which decreased the speed of electron transfer on the donor side, resulting in premature leaf senescence, whereas there were no significant differences in light treatments with a higher proportion of red light.

In the O–J phase, there was a fast rise of the J-step in the OJIP curve in the B and R1B2 lights. It is related to the redox state of Q_A, depending on the balance between its reduction by P680 and its reoxidation by Q_B (Strasser *et al.* 1995, Boisvert *et al.* 2006). The closure of the active reaction center in the B and R1B2 lights was vividly larger than that in the CK at 2 ms in the OJIP curve (V_J), whereas the other lights showed no difference with CK. This indicated that there was greater closure in the active reaction center irradiated by a higher proportion of blue LED light. Previous studies concluded that salt stress and drought stress conditions produced a higher increase in the J-step and V_J increased significantly, which demonstrates that electrons transferred from Q_A to Q_B on the PSII acceptor side were blocked (Chen *et al.* 2014, Jiang *et al.* 2020, Mihalhević *et al.* 2021). In this study, the rising J-step in B and R1B2 treatments contributed to the enormous accumulation of Q_A^- in the PSII reaction center because the flow of electrons outside Q_A was blocked.

In the O–I phase, the pool size of the end electron acceptors at the PSI acceptor side was reflected by the maximal amplitude of $W_{OI} \geq 1$ (Oukarroum *et al.* 2009). The maximal amplitude of $W_{OI} \geq 1$ was observed under irradiation by R2B1 lights, and that of the B light was the lowest from the six different lights used in this study. It indicated that B light could result in a smaller pool size of the end electron acceptor at the PSI acceptor side relative to the other treatments. According to Strasser *et al.* (1995), the reason for reducing the PQ pool under B treatment is due to the existence of fast and slow reducing PQ centers, and due to the inhibition in the reduction of Q_A to Q_A^- of the RC complex in different redox states ($Q_AQ_B^{2-}$).

Furthermore, our results showed that the JIP-test parameters, which quantified the conformation, structure, and function of photosynthetic apparatus, were significantly lower in the B treatment than those in the other treatments. The saffron plants were significantly inhibited by blue light as shown by the performance index (PI_{total}), photosynthetic capacity (φ_{Po}, φ_{Ro}, φ_{Eo}), and electron transport (ET_0/RC, ψ_{Ro}, ψ_{Eo}, δ_{Ro}); decreased number of reaction centers (RC/CS_m), and increased excitation energy dissipation (DI_0/RC) (Li *et al.* 2015, He *et al.* 2018).

A comprehensive analysis of the results suggests that B light results in a substantial increase in the proportion of inactivated PSII reaction centers in saffron and thus, decreased capacity of electron transport, photochemical efficiency, and the inhibited reduction of Q_A to Q_A^- of the RC complex.

Conclusions: We demonstrated that supplementation with R2B1 light benefited the growth of saffron plants, which developed elongated leaves, accumulated chlorophyll, and promoted photosynthesis characteristics. Therefore, we recommend the use of R2B1 LED light as a supplementary light for saffron cultivation. In this study, along with a decrease in the red to blue light ratio, particularly in the B treatment, negative effects on the growth of leaves decreased the chlorophyll content and inhibited photosynthesis, which was evident from the significant reduction of P_N, g_s, and E, and the acceleration of earlier leaf senescence at 120 d. There was a rapid rise in the K-point in the OJIP curve under B LED light which resulted in the OEC inactivation. B LED light affected the reduction of PSII, resulting in damage to electron transport and the energy flux of reduction in Q_A to Q_A^-, as well as the existence of reducing PQ centers. Overall, saffron plants were inhibited by blue light, which is documented in the photochemical efficiency, photosynthetic capacity, electron transport, and decreased number of reaction centers. This study unveiled new insights to explore the critical physiological factors of the morphological differences of saffron leaves irradiated by LED light and provided theoretical guidance for the agricultural practices of saffron.

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