

Responses of the photosynthetic characteristics and chloroplast ultrastructure of Welsh onion (*Allium fistulosum* L.) to different LED light qualities

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Abstract

The optimized illumination of plants using light-emitting diodes (LEDs) is beneficial to their photosynthetic performance. Because of this, in recent years LEDs have been widely used in horticultural facilities. However, there are significant differences in the responses of different crops to light quality. The influence of light quality on photosynthesis needs to be further explored to provide theoretical guidance for the adjustment of the light environment in industrial crop production. This study tested the effects of different qualities of LED lighting (white, W; blue, B; green, G; yellow, Y; and red, R) with the same photosynthetic photon flux density ($300 \mu\text{mol}/\text{m}^2\cdot\text{s}$) on the growth and development, photosynthesis, chlorophyll fluorescence characteristics, leaf structure, and chloroplast ultrastructure of Welsh onion (*Allium fistulosum* L.) plants. The results showed that the plant height, leaf area, and fresh weight of plants in the W and B treatments were significantly higher than those in the other treatments. The photosynthetic pigment content and net photosynthetic rate (P_n) in the W treatment were significantly higher than those in the monochromatic light treatments, while the transpiration rate (E) and stomatal conductance (G_s) were the highest in the B treatment, and the intercellular CO_2 concentration (C_i) was the highest in the Y treatment. Among the chlorophyll fluorescence characteristics tested, the non-photochemical quenching coefficient (NPQ) was the highest in the Y treatment, while the maximum photochemical efficiency of photosystem II (PSII) under dark adaptation (F_v/F_m), maximum photochemical efficiency of PSII under light adaptation (F_v'/F_m'), photochemical quenching coefficient (q_P), actual photochemical efficiency (Φ_{PSII}), and apparent electron transport rate (ETR) all differed among treatments in the following order: $W > B > R > G > Y$. Both leaf structure and chloroplast ultrastructure showed the most complete development in the B treatment. In summary, in addition to W light, B light significantly improved the photosynthetic efficiency of Welsh onion, whereas Y light significantly reduced the photosynthetic efficiency of this plant.

Background

Light is not only the primary source of energy for photosynthesis in plants, but is also an important signal for plant growth and development [1]. Light intensity, light quality, and photoperiod can regulate plant growth and development [2]. Johkan [3] found that the net photosynthetic rate (P_n) in the leaves of *Lactuca sativa* plants irradiated with green light from a light-emitting diode (LED) at a photosynthetic photon flux (PPF) of $200 \mu\text{mol}/\text{m}^2\cdot\text{s}$ was significantly higher than that at a PPF of $100 \mu\text{mol}/\text{m}^2\cdot\text{s}$, and the P_n of plants irradiated with G510 light (peak wavelength: 510 nm; band width at half peak height: 18 nm) was the highest among all the light sources they tested. Many processes can also be regulated by adjusting the wavelength of light to which plants are exposed, such as seed germination, photomorphogenesis, photosynthesis, carbon and nitrogen metabolism, biomass accumulation, chloroplast ultrastructure, and leaf anatomical structure[4-9]. Studies have shown that the regulation of red light and the far-red light ratio can regulate the flowering time of *Arabidopsis*, and also provided evidence of the existence of light quality pathways regulating plant flowering times [10].

Photosynthesis is an important biological process for maintaining plant life, and has played a very important role in the evolution of the Earth's ecosystems. Increasing rates of photosynthesis is critical to increasing crop yields to meet rising human needs for food [11, 12]. Chloroplast development and chlorophyll metabolism are important activities involved in photosynthesis in green plants. Previous studies have demonstrated the existence of chlorophyll synthesis-related enzymes that are key regulators of chloroplast development [13, 14]. It was previously found that the rate of photosynthesis in cucumber seedlings was significantly higher under white light than that under red, blue, yellow, and green light, and that the morphology, growth, and the photosynthetic rates of these plants under different monochromatic light treatments were significantly different [15]. It was also previously shown that RGB light (33% red, 33% green, and 33% blue) and RB light (66% red and 33% blue) reduced the plant height, plant biomass, and leaf area of tomato plants compared to those of plants grown under white light [16]. In a study of the effects of different light quality treatments on tobacco, monochromatic light treatments reduced tobacco growth, Pn, stomatal conductance, intercellular CO₂, and transpiration rates compared to those of plants grown under white light [8]. In another study of the effects of light quality (white, blue, yellow, and red light) on the growth and photosynthesis of *Camptotheca acuminata* seedlings, it was found that red light promoted the development of chloroplasts and improved the photosynthetic efficiency of the seedlings of this plant [17].

Ribose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO; EC 4.1.1.39) is a key enzyme in plant photosynthesis that controls both CO₂ and carbon fixation. The Calvin cycle and the photorespiration cycle are shunted by this process, and the relative magnitudes of their activities directly affect the photosynthetic rate [18]. Gao [19] found that when the ratio of red to blue light was 4:1, the ribose-1,5-bisphosphate carboxylase (RuBPCase) activity in purple lettuce was significantly higher than that in control plants and those in other light treatments.

Although previous studies have determined the effects of light quality on the growth, physiology, and morphology of various plant species, few studies have reported upon the responses of the growth, photosynthetic characteristics, and flavor of Welsh onion to different LED light qualities. Welsh onion (*Allium fistulosum* L.) is an important seasoning vegetable. In recent years, the scale of the production of Welsh onion in industrial facilities has been expanding. To create good environmental conditions for the growth of crops in such facilities, previous studies have been conducted on the relationships between light quality and the growth, photosynthetic characteristics, carbon and nitrogen metabolism, and volatile production of other plants. Research by Lin [20] showed that the root fresh weight and dry weight of lettuce treated with combined red-blue-white light (RBW) and full-spectrum light (FL) were higher than those of lettuce treated with RB light. Zhang [21] found that the content of sucrose, fructose, and glucose in peach fruits grown under natural light was higher than that in those grown covered with blue film, red film, green film, and yellow film. In addition, previous studies also examined the responses of plant volatiles to different light qualities. For instance, basil plants grown under light at blue-red-yellow (BRY) or blue-red-green (BRG) wavelengths evaporated higher levels of monoterpenoid volatiles, while basil plants grown under a combined far-infrared-blue-red (far-RBR) treatment evaporated even higher levels of most

sesquiterpenoid volatiles [22]. The main flavor of Welsh onion comes from an organic sulfide, which is an important indicator of its nutritional quality [23]. The organic sulfide content of the plant can be expressed as the content of pyruvic acid, its decomposition product [24]. The objective of this study was to test the effects of different LED light qualities on the photosynthetic characteristics and chloroplast ultrastructure of Welsh onion plants.

Results

Response of growth and development of Welsh onion to different LED light qualities

The number of leaves, LA, plant height, cauloid diameter, and cauloid FW of Welsh onion plants were significantly higher after 30 days under W light than under any monochromatic light treatment, and the growth of plants in the B treatment was significantly higher than that under all the other monochromatic light treatments. The cauloid and leaf dry matter content of plants in the B treatment were slightly higher than those of plants in the W treatment, indicating that the water content of the Welsh onion was higher in the W treatment. The growth of plants under the monochromatic light treatments differed in the following order: B > R > G > Y (Fig. 1B, Table 1).

Response of the photosynthetic pigment content in Welsh onion to different LED light qualities

The content of chlorophyll a and chlorophyll b in the W treatment were significantly higher than those in all the monochromatic light treatments, and among the monochromatic light treatments these were the highest in the B treatment (Table 2). Chlorophyll b (Chl b) plays an important role in adapting plants to low-light conditions. In low light, plants synthesize more Chl b, which helps to form a larger light-harvesting system as an adaptation to low-light environments [25]. The chlorophyll a/b ratio was significantly higher in all treatments than that in the G one except in the B and Y treatments, and the difference in this ratio between the W and Y treatment was not significant. The trends in carotenoid content and chlorophyll content were consistent. This indicates that, in addition to the full light spectrum (W treatment), the light quality in the B treatment could promote increases in the chlorophyll a, chlorophyll b, and carotenoid content of Welsh onion. This also shows that the G treatment could enhance the absorption ability of Welsh onion in low-light conditions.

Responses of photosynthetic parameters of Welsh onion to different LED light qualities

Photosynthetic parameters were measured under white, blue, red, green, and yellow light for about 5 min each. The P_n of Welsh onion leaves was the highest in the W treatment, and then decreased in turn in the B, R, G, and Y treatments, respectively. On the 30th day of treatment, the leaf P_n was 6.45 $\mu\text{mol}/\text{m}^2\cdot\text{s}$, 5.54 $\mu\text{mol}/\text{m}^2\cdot\text{s}$, 3.87 $\mu\text{mol}/\text{m}^2\cdot\text{s}$, 3.50 $\mu\text{mol}/\text{m}^2\cdot\text{s}$, and 4.40 $\mu\text{mol}/\text{m}^2\cdot\text{s}$ in the W, B, G, Y, and R treatments, respectively (Fig. 2A). The G_s and transpiration rate (E) were significantly higher in the B treatment than in the W treatment and monochromatic light treatments, and these decreased in turn in the Y, G, and R treatments, respectively (Fig. 2B-C). The C_i in the Y and G treatments was significantly higher than that in

all other treatments, and was the lowest in the W treatment (Fig. 2D). These results showed that the B treatment could improve the ability of Welsh onion plants to perform photosynthetic gas exchange.

Responses of chlorophyll fluorescence parameters in Welsh onion to different LED light qualities

The F_v/F_m and F_v'/F_m' of Welsh onion in all light quality treatments except the W treatment were significantly higher than those in the Y treatment, but those in all other combinations of treatments were not significantly different (Fig. 3A-B, Fig. 4). The qP was significantly higher in the W treatment than in all of the other treatments. Among the monochromatic light treatments, the qP in the B treatment was the highest, and that in the Y treatment was the lowest (Fig. 3C). The $\Phi PS II$ and ETR showed consistent trends among treatments with those in qP , and were both significantly higher in the W treatment than in the monochromatic light treatments, and decreased sequentially in the B, R, G, and Y treatments, respectively (Fig. 3D-E). The NPQ and qP showed opposite trends, with the NPQ being the highest in the Y treatment, and the lowest in the W treatment (Fig. 3F). These results indicated that among the monochromatic light treatments, the B treatment could increase the proportion of the reaction centers in PSII opening under light adaptation, enhance PSII reaction center activity, and increase the electron transfer rate, while the Y treatment increased the heat dissipation capacity of Welsh onion plants.

Responses of leaf anatomy and chloroplast ultrastructure in Welsh onion to different LED light qualities

Welsh onion (*Allium fistulosum* L.) plants have fistular leaves. The fistular lamina of Welsh onion leaves changes from being solid to hollow during development, and the cells around the cavity break up until the remaining 1-2 layers of cells from the palisade show cell wall residues ('arrowheads') [26]. Through the observation of leaf slices after red-green staining, the palisade tissue cells in each layer of the B-treated leaves in this study were found to have the same size and tight arrangement, and the chlorophyll in them was dense, which meant they could use the spaces in the leaf to more efficiently improve the absorption efficiency of light energy, thereby contributing to improved photosynthesis. On the other hand, in the W-, R-, and G-treated Welsh onion leaves, the palisade tissue cells were arranged in a relatively disordered manner, and in the Y treatment their arrangement was loose. Differences in leaf vascular bundle sizes were found in the following order: $W > B > R > G > Y$. There were no significant differences in the spongy mesophyll tissue thickness or arrangement among treatments (Fig. 5).

Chloroplasts are the locations where chlorophyll is found and photosynthesis occurs in plant cells. If chlorophyll synthesis is reduced or blocked, this will result in a change in chloroplast structure [27]. The different light quality treatments greatly affected the development of chloroplasts in the leaves of Welsh onion in this study. The size and shape of the chloroplasts in the mesophyll cells of Welsh onion were observed by transmission electron microscopy after sampling them on the 30th day of treatment with different LED light qualities. The normal shape of the chloroplast is fusiform or elliptical, and they are arranged along the plasma membrane in Welsh onion cells. In normal chloroplasts, the structure of the granular sheets (grana lamellae) in the chloroplasts is clearly visible and runs parallel to the long axis of the chloroplast, and the thylakoids are closely packed and arranged in a neat and orderly manner; such

normal chloroplasts were observed in the W and B treatments herein (Fig. 6A1-B3). In addition, the thylakoid membranes in B-treated plants' leaf cells grew the most, which means that the B-treated Welsh onion plants had a greater light-capturing ability, and thus an improved energy conversion efficiency of the photosynthetic membrane [28]. However, the chloroplasts of Y-treated Welsh onion leaves became smaller, and the granular lamellae of the thylakoids in the chloroplasts degraded, resulting in them having decreased photosynthetic capacity (Fig. 6D1-D3). Our results indicated that the chloroplasts of cells in leaves treated with B and R light were intact and still contributed well to photosynthesis, while the development of chloroplasts was inhibited in the Y treatment.

Response of RuBPCase activity in Welsh onion to different LED light qualities

RuBPCase is a key enzyme for photosynthesis. Different light qualities had significant effects on the activity of the RuBPCase in Welsh onion in this study. The activities of RuBPCase were 28.21 nmol/min/mg prot, 24.39 nmol/min/mg prot, 20.91 nmol/min/mg prot, 18.31 nmol/min/mg prot, and 23.57 nmol/min/mg prot in the W, B, G, Y, and R treatments, respectively. Among the different monochromatic light treatments, the B treatment increased the RuBPCase activity in Welsh onion, while the Y treatment inhibited RuBPCase activity (Fig. 7). These results suggested that the B treatment could improve the RuBPCase activity, which in turn would affect the Pn of the Welsh onion plants.

Discussion

The light environment in which crops are held is one of the most important environmental factors affecting crop growth and development. It directly affects the shapes of plants because light intensity and light quality act as signaling factors during development [29]. Photosynthesis is the most important chemical reaction on Earth, and is the basis for the survival of all living things. Light is the driving force behind photosynthesis [30], and the quality or spectral composition of light is an important property thereof. The wavelength of the visible light spectrum is 380-780 nm, while light with a wavelength shorter than 380 nm is ultraviolet light, and that with a wavelength longer than 780 nm is far-infrared light. In the natural environment, the spectral composition of the light experienced by plants is constantly changing, with there being more blue light in cloudy and daytime periods, more red light in the morning and evening, and a strong influx of white light at noon, and with even more variation introduced by weather [31]. Under a plant canopy, the spectral quality of the light also changes, which can be used as an important signal for light competition responses in plants. Physiological studies have shown that plants can perceive the quality of the light reflected from the surrounding environment, and use it as an accurate predictor of future competition, even inducing morphological responses to avoid light competition before direct shading actually occurs [32].

In this study, there were significant differences in the growth and development of Welsh onion plants among LED light treatments with different wavelengths. We found that the whole-spectrum W-treated Welsh onion plants grew the best, which is consistent with the conclusions of previous studies done on cucumber [15]. Among the monochromatic light treatments tested, the plants grown in the B treatment

were more compact, whereas those grown in the G and Y treatments were not as compact. This may have been due to the different responses of the leaves to different optical signals, which would be consistent with the results of previous studies done on rice and lettuce [33, 34]. However, different results were reported for studies done on *Camptotheca acuminata* Decne. seedlings, wheat, and other crops [6, 35], which may have been due to differences in the responses of different species to variation in light quality. In a previous study [36] of the effects of combined red-blue light on cucumber seedlings, the growth rate and leaf area were reduced as the proportion of blue light in the environment decreased. Plant growth rate was the lowest in that study in the 0% B:100% R treatment, and the fastest in the 100% B:0% R treatment, which may have been related to a variety of morphological and physiological factors [36].

Previous studies have shown that photosynthetic pigments can absorb and transmit light energy, which makes these pigments the material basis for photosynthesis in plants. Light quality affects the synthesis of photosynthetic pigments, which in turn affects the photosynthesis of plants, and thus plays an important role in regulating plant growth and development [37, 38]. The pigments found in plant leaves are closely related to their physiological functions. It was previously found that a reduction in CO₂ assimilation occurred under combined rose-blue light, which was related to the decreased photosynthetic pigment content of the tested plants [39]. Chlorophyll absorbs light energy and transfers it to the chloroplasts for photosynthesis [40]. In this study, the P_n of Welsh onion seedlings grown under monochromatic light decreased significantly compared to that of seedlings grown under W light, especially under Y and G light (Fig. 2A). This is consistent with the results of previous studies of cucumber and *Acacia mangium* seedlings [41, 42]. In the present study, the P_n of Welsh onion was significantly associated with its chlorophyll content and RuBisCO content. The transpiration rate (E) and stomatal conductance (G_s) were the highest under B light, probably because the stomata of the seedlings exposed to blue light developed well, meaning that the stomatal conductance and nitrogen accumulation were high in them compared with those in seedlings raised under other monochromatic light treatments [43].

RuBisCO, acting as RuBPCase, is known to be a key enzyme in the Calvin cycle, the nature of which determines the photosynthetic efficiency and ultimate productivity of photosynthetic organisms. Previous studies have shown that light quality affects RuBPCase activity in algae [44, 45]. In our experiments, the higher rate of photosynthesis observed in the B treatment may have been related to the chlorophyll content, light energy conversion efficiency, and RuBPCase activity of plants in this treatment, which were all high and thus would have promoted good Welsh onion growth.

The measurement of the chlorophyll fluorescence of green plants reflects their photosynthetic potential in a complex manner [46]. Green plants absorb light, some of which is used for photosynthesis, while some re-emerges in the form of chlorophyll (Chl) fluorescence, and some is used for heat dissipation [47]. The F_v/F_m , ETR, and qP parameters are often used to indicate the maximum photochemical efficiency of PSII and the ratio of reaction centers in PSII that are oxidated (open), which are indicators of photosynthetic efficiency. NPQ is one of the important mechanisms used by plants to dissipate excess light energy. This parameter indicates the ability of chloroplasts to dissipate excess excitation energy in the form of

superheat [48]. In addition, Φ PSII is often used to indicate the quantum yield of electron transfer in plant photosynthesis, reflecting the actual primary light energy capture rate when the reaction centers are partially closed. In this study, among the monochromatic light treatments, the Fv/Fm, ETR, qP, and Φ PSII were the highest in B-treated Welsh onion plants, while the NPQ was decreased in these. Therefore, we propose that treatment with B light increased the rate of photosynthesis in Welsh onion, but reduced the heat dissipation ability of PSII in this plant. It was thus shown in this study that B light is beneficial to Welsh onion because it improves the light energy conversion efficiency of this plant and allows it to accumulate more energy for carbon assimilation in the dark reactions. In a similar study, *Phalaenopsis* had lower Fv/Fm values in a 0% B:100% R light treatment compared to that in treatments containing more blue light [49].

In the present study, the anatomical structure of the leaves of Welsh onion was significantly changed by treatments with different LED light qualities. In the W treatment, loosely arranged palisade mesophyll cells were observed, and the spaces among the palisade cells were the largest observed (Fig. 5A), which was similar to the findings of a previous study of potato (*Solanum tuberosum* L.) leaves [50]. Sæbø [51] showed that when the *in vitro* culture of *Betula pendula* Roth was carried out under light of different quality, the areas of epidermal cells were the largest under blue light irradiation, and the smallest under red light. In the present study, on the 30th day of treatment, the number of chloroplasts per cell was the highest in the plants grown under B light, and the number of grana lamellae in each chloroplast was the highest (Fig. 6B1-B3), which was consistent with the results of previous studies done on cucumber leaves [52].

Conclusions

The growth and development of plants is strongly influenced by the spectrum of light in their growing environment. In this study, the growth, photosynthetic characteristics, and chlorophyll fluorescence characteristics of Welsh onion grown under LED light source of different quality were studied. The purpose of this study was to reveal the effects of light quality on the photosynthesis of Welsh onion, as well as to provide a theoretical basis for the regulation of light environments used in the growth of Welsh onion.

As expected, the growth and morphology of Welsh onion plants were altered by growing them under different light spectra, and different light quality treatments had significant effects on photosynthesis-related processes. In this study, the full-spectrum W treatment was the most beneficial for the growth of Welsh onion. Among the monochromatic light treatments, the chlorophyll content, Chl a/Chl b ratio, net photosynthetic rate, stomatal conductance, and transpiration rate were the highest in the B treatment, indicating that B light is beneficial to the photosynthesis of Welsh onion. At the same time, it can be seen from the leaf structural changes observed that R light may play an important role in chloroplast development and delaying leaf senescence. However, the Y treatment induced NPQ, affecting plant morphology, destroying leaf tissue and thylakoid membrane structure, reducing the photosynthetic pigment content, and significantly reducing the net rate of photosynthesis. In summary, different

monochromatic light qualities were found to each play unique roles in the growth and photosynthesis of Welsh onion.

Methods

Materials and treatments

The experiment was carried out in the light quality culture room of the College of Horticulture Science and Engineering, Shandong Agricultural University, Shandong, China (longitude: 117.12°E; latitude: 36.19°N) during October and November 2018. The Welsh onion variety tested was 'Yuanzang', which was seeded in 50-hole trays. The cultivation substrate was a 6:3:1 mixture of charcoal: perlite: vermiculite. Seedlings were watered with 1/2 Hoagland nutrient solution every 3 days after sowing. When the seedling height was about 5 cm, they were thinned so that there was only 1 seedling per hole, and when the seedling height was about 15 cm 2-3 pieces of true leaves from the seedlings were taken and placed in treatments under LEDs with different light qualities. The original source of the welsh onion was Tai'an Taishan Seed Industry Technology Co., Ltd. Dimming plant lamps (Huizhou Kedao Technology Co., Ltd.) were used with different light qualities as follows: white light (W), blue light (B), green light (G), yellow light (Y), and red light (R); these formed 5 treatments, among which the white light treatment was used as a control. All the processes are legitimate. The spectral characteristics of the LED sources were measured with an UNSPEC-DCTM spectrum analyzer (PP-SYSTEMS, UK). The band with was 300-1100 nm, and the scanning wavelength interval was 3.3 nm. The spectral characteristics of each light quality treatment are shown in Fig. 1A-B.

By adjusting the light intensity of the LED light sources, the light intensity at each treated plant's canopy was maintained at $301.6 \pm 12.7 \mu\text{mol}/\text{m}^2 \cdot \text{s}$. The day/night temperature was controlled to remain at 25 °C/18 °C, respectively, the relative humidity of the air was $65.2 \pm 4.5\%$, and the light/dark (L/D) photoperiod was set to 12 h L/12 h D. Each treatment contained 20 plants, and all treatments and assays were repeated 5 times.

Measurement of morphological and physiological characteristics

Welsh onion plants grown in different light quality treatments were randomly sampled and measured 30 days after planting. Measurements taken of them included their leaf number, leaf area (LA), plant height, cauloid diameter, leaf fresh weight (FW), cauloid FW, root FW, and aboveground dry matter content. The plant height and cauloid diameter of the Welsh onion plants were measured with a ruler and Vernier caliper, respectively. The LA was determined using a LI-3000C leaf area meter (LI-COR Biosciences, USA). The Welsh onion samples were placed in a dry box, dried at 75 °C for 48 h, and then weighed to measure the aboveground dry matter content of the plants.

Measurement of photosynthetic pigment content

The chlorophyll content of the Welsh onion leaves was determined by 80% acetone extraction. A fresh sample of 0.2 g of the third leaf blade was weighed and placed in a 20 mL test tube containing 5 mL of absolute ethanol and 5 mL of 80% acetone, and left to stand in the dark for 24 h. The optical density (OD) was measured with a UV-1200 spectrophotometer (Shimadzu, Japan) at 470 nm (OD_{470}) for carotenoids, 663 nm (OD_{663}) for chlorophyll a (Chl a), and 645 nm (OD_{645}) for chlorophyll b (Chl b), and was then used to calculate the content of each respective pigment in the leaves using the following formulas [53, 54]:

$$\text{Chl a (mg g}^{-1}\text{)} = (12.72 \text{ } OD_{663} \text{ nm} - 2.59 \text{ } OD_{645} \text{ nm}) \text{ V}/1,000 \text{ W};$$

$$\text{Chl b (mg g}^{-1}\text{)} = (22.88 \text{ } OD_{645} \text{ nm} - 4.67 \text{ } OD_{663} \text{ nm}) \text{ V}/1,000 \text{ W};$$

$$\text{Carotenoids (mg g}^{-1}\text{)} = (1,000 \text{ } OD_{470} \text{ nm} - 3.27 \text{ Chl a} - 104 \text{ Chl b}) \text{ V}/(229 \times 1,000 \text{ W}),$$

where V is the total volume of acetone extract (ml), and W is the fresh weight (g) of the sample.

Measurement of photosynthetic characteristics and chlorophyll fluorescence

On the 30th day of each treatment, the functional third leaves of the Welsh onion plants were selected and measurements of the net rate of photosynthesis (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) were taken from them using a Li-6800 portable photosynthetic apparatus (Li-COR, USA) following the methods of Li [55], with slight modifications. To measure the CO_2 fixation by photosynthesis under different illumination conditions, the gas exchange characteristics of the functional leaves were measured under white, blue, red, green, and yellow light sources. The leaf chamber temperature and leaf CO_2 concentration were maintained at 25 °C and 400 $\mu\text{mol/m}^2\cdot\text{s}$, respectively, during these measurements, and the vapor-pressure deficit (VPD) in the leaf chamber was kept at 1.0 kPa. When the P_n reached a steady state at each light intensity level, it was recorded as the P_n for that light intensity. These measurements were taken 5 times for each treatment, and the average value was calculated for each treatment's photosynthetic parameters. The RuBPCase activity of RuBisCO in each treatment was determined using an enzyme-linked immunosorbent assay (ELISA) kit (Suzhou Keming).

The chlorophyll fluorescence of the third fully expanded functional leaf of the Welsh onion plants in different treatments was measured using an M-series modulated chlorophyll fluorescence imaging system (MINI-IMAGING-PAM, Walz, Effeltrich, Germany). To do so, the fluorescence parameters were first determined after dark adaptation for 20 min. Initial fluorescence (F_o) was measured after induction by a weak modulation (0.05 $\mu\text{mol/m}^2\cdot\text{s}$) after dark adaptation, followed by excitation with a strong saturation pulse (6000 $\mu\text{mol/m}^2\cdot\text{s}$, pulse time = 2 s) to produce and measure the maximum fluorescence (F_m). Next, for light adaptation, the F_o and F_m' (the maximum fluorescence yield obtained when the light-adapted sample was exposed to the saturation pulse) were directly measured under each LED light before the actinic light was turned on, and then a series of saturation pulses was started under each LED light. Multiple strong saturated flash pulses were applied (6000 $\mu\text{mol/m}^2\cdot\text{s}$, pulse time = 2 s), and then the

fluorescence yield (Ft) and Fm' under adaptation with each LED light were measured every 20 s until pulse termination. The average values of the last 6 flashes (after a substantially steady state was reached after 10 flashes) were then taken. At the time of measurement, the measurements from 5 plants were averaged for each treatment. The measured indicators included the Fo, Fm, and Ft. Other fluorescence parameters were calculated after Genty [56] as follows:

Maximum photochemical efficiency of photosystem II (PSII) under dark adaptation (F_v/F_m) = $(F_m - F_o)/F_m$;

Maximum photochemical efficiency of PSII under light adaptation (F_v'/F_m') = $(F_m' - F_o')/F_m'$;

Actual photochemical efficiency (Φ_{PSII}) = $(F_m' - F_s)/F_m'$;

Non-photochemical quenching coefficient (NPQ) = $1 - (F_m' - F_o')/(F_m - F_o)$;

Photochemical quenching coefficient (qP) = $(F_m' - F_t)/(F_m' - F_o')$;

Apparent electron transport rate (ETR) = $\Phi_{PSII} \cdot PAR \cdot 0.5 \cdot 0.84$,

where PAR is $300 \mu\text{mol}/\text{m}^2 \cdot \text{s}$.

Observation of the leaf anatomy and chloroplast ultrastructure of Welsh onion

On the 30th day of treatment under different light qualities, paraffin section of samples (5 mm × 5 mm) were taken, fixed with FAA (formalin–acetic acid–alcohol) fixative, dehydrated with an alcohol and xylene series, embedded in paraffin, cross-sectioned to a thickness of 10 μm , and red-solid green stained. The total thickness of the transverse sections, as well as the thickness of the upper epidermis, palisade mesophyll tissue, and spongy mesophyll tissue, were measured under a light microscope using a micrometer.

On the 30th day of treatment under different light qualities, pieces of functional leaves were sampled (1 mm × 1 mm), quickly placed in a 2.5% glutaraldehyde fixative solution, and evacuated with a vacuum pump. They were then allowed to sink to the bottom of the solution, left at room temperature (25 °C) for 2 h, and then transferred to a refrigerator and stored at 4 °C. They were then rinsed 3 times with 0.1 M phosphate buffer (PB, pH = 7.4) for 15 min each time. Samples were fixed with 1% citric acid in 0.1 M phosphate-buffered saline (PBS, pH = 7.4) at room temperature (25 °C) for 5 h, and then rinsed again 3 times with 0.1 M PB (pH = 7.4) for 15 min each time. The leaf tissue was then subjected to a dehydration-infiltration-embedding-slicer (Leica, LeicaUC7) section-staining-transmission electron microscope (HITACHI, HT7700) for observation and image analysis.

Data analysis

Sampling of plants followed the principle of random sampling in this study. The test data were processed, plotted, and statistically analyzed using Excel 2016 and DPS software, and tested for

significant differences ($P \leq 0.05$) among treatments using Duncan's new multiple range test.

Abbreviations

Chl a: Chlorophyll a; Chl b: Chlorophyll b; Pn: Net photosynthetic rate; E: Transpiration rate; Gs: Stomatal conductance; Ci: Intercellular CO₂ concentration; VPD: Vapor-pressure deficit; Fo: Initial fluorescence; Fm: maximum fluorescence; PSII: Photosystem II; Fv/Fm: Coefficient maximum photochemical efficiency of photosystem II under dark adaptation; Fv'/Fm': Maximum photochemical efficiency of PSII under light adaptation; NPQ: Non-photochemical quenching; qP: Photochemical quenching coefficient; Φ PSII: Actual photochemical efficiency; ETR: Apparent electron transport rate, E: epidermis; PT: palisade tissue; ST: spongy tissue; VB: vascular bundle, Ch: chloroplast; GL: grana lamella; SL: stroma lamella.

Declarations

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Authors' contributions

GS, LXN, LY and XK conceived and designed research. GS conducted experiments, analyzed data and wrote the manuscript. GS, CBL, CHZJ and XK modified the paper. All authors have read and approved the manuscript.

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Availability of data and materials

All data generated or analysed during this study are included in this published article.

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare that they have no conflict of interest.

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Tables

Table 1 Response of Welsh onion growth and development to different LED light qualities. Values are means of four replicates $\pm$ standard deviation (SD). Different letters (a, b, c, d) in the same column indicate significant differences among treatments at $P \leq 0.05$ according to Duncan's new multiple range test. W: white light; B: blue light; G: green light; Y: yellow light; R: red light.

Light quality	Leaf number	Leaf area (cm ²)	Plant height (cm)	Cauloid diameter (mm)	Leaf FW (g/plant)	Cauloid FW (g/plant)	Root FW (g/plant)	Cauloid and leaf dry matter (%)
W	4.60 $\pm$ 0.55a	151.61 $\pm$ 3.34a	49.80 $\pm$ 1.26a	11.63 $\pm$ 0.43a	19.48 $\pm$ 0.78a	10.88 $\pm$ 1.55a	2.32 $\pm$ 0.10a	9.82 $\pm$ 0.17b
B	4.40 $\pm$ 0.55ab	142.60 $\pm$ 6.25b	47.44 $\pm$ 1.24b	9.66 $\pm$ 0.28b	14.34 $\pm$ 0.64b	9.04 $\pm$ 0.22b	1.83 $\pm$ 0.10b	10.08 $\pm$ 0.10a
G	4.20 $\pm$ 0.45ab	122.14 $\pm$ 2.12c	51.00 $\pm$ 1.91a	8.91 $\pm$ 0.17c	13.65 $\pm$ 0.77b	8.99 $\pm$ 0.43b	1.85 $\pm$ 0.07b	9.37 $\pm$ 0.10c
Y	3.80 $\pm$ 0.45c	99.66 $\pm$ 5.55d	44.44 $\pm$ 1.43c	8.29 $\pm$ 0.27c	11.47 $\pm$ 0.52c	7.24 $\pm$ 0.25c	1.55 $\pm$ 0.11b	8.97 $\pm$ 0.24d
R	3.40 $\pm$ 0.55bc	114.15 $\pm$ 4.57c	47.44 $\pm$ 2.11b	8.04 $\pm$ 0.09c	12.07 $\pm$ 0.56c	7.49 $\pm$ 0.19c	1.66 $\pm$ 0.05b	9.01 $\pm$ 0.12d

Table 2 Responses of the content of different photosynthetic pigments in Welsh onion to different LED light qualities. Values are means of five replicates $\pm$ SD. Different letters (a, b, c, d) in the same column indicate significant differences among treatments at $P \leq 0.05$ according to Duncan's new multiple range test. W: white light; B: blue light; G: green light; Y: yellow light; R: red light.

light quality	chlorophyll a (mg $\cdot$ g ⁻¹)	chlorophyll b (mg $\cdot$ g ⁻¹)	Carotenoid (mg $\cdot$ g ⁻¹)	chlorophyll a+b (mg $\cdot$ g ⁻¹)	chlorophyll a/b
W	0.61 $\pm$ 0.005a	0.27 $\pm$ 0.002a	0.20 $\pm$ 0.001a	0.88 $\pm$ 0.006a	2.24 $\pm$ 0.016ab
B	0.54 $\pm$ 0.001b	0.23 $\pm$ 0.002b	0.17 $\pm$ 0.002b	0.77 $\pm$ 0.003b	2.32 $\pm$ 0.021a
G	0.44 $\pm$ 0.003d	0.20 $\pm$ 0.0050d	0.15 $\pm$ 0.001d	0.65 $\pm$ 0.005d	2.18 $\pm$ 0.065b
Y	0.39 $\pm$ 0.005e	0.17 $\pm$ 0.003e	0.12 $\pm$ 0.001e	0.56 $\pm$ 0.003e	2.30 $\pm$ 0.066a
R	0.49 $\pm$ 0.001c	0.22 $\pm$ 0.001c	0.16 $\pm$ 0.001c	0.70 $\pm$ 0.001c	2.25 $\pm$ 0.018ab

Figures

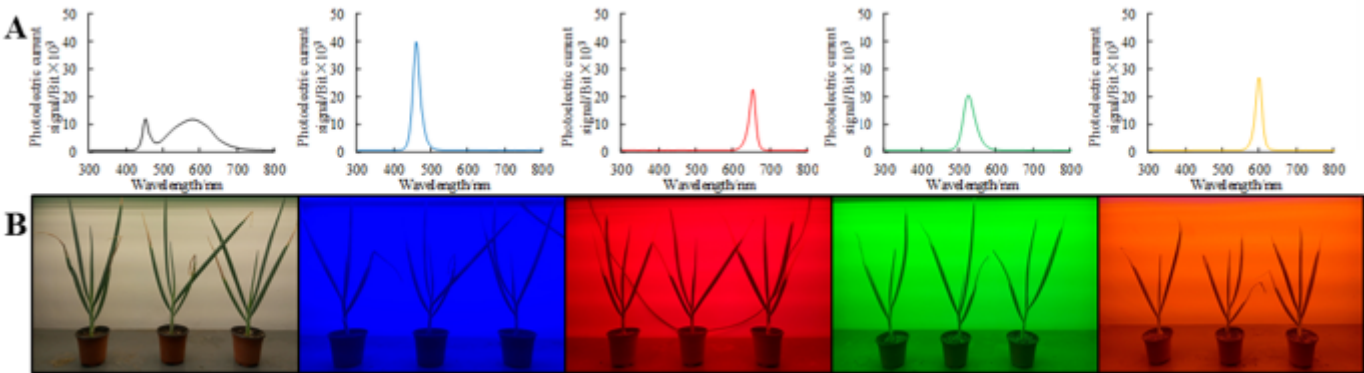
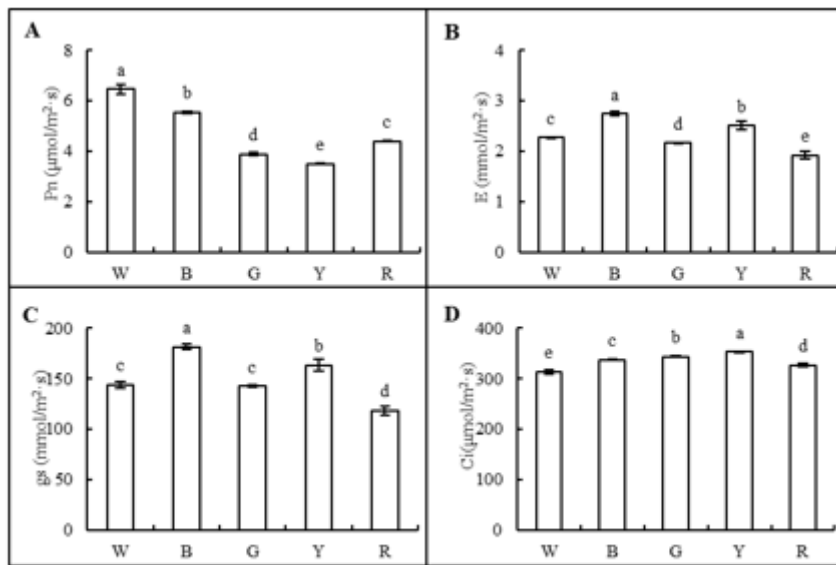


Figure 1

(A) Characteristics of the respective LED irradiance spectra in the different treatments; (B) the different LED light quality treatments tested.



light: G: green light; Y: yellow light; R: red light.

Figure 2

Responses of the photosynthetic parameters of Welsh onion to different LED light qualities, including: (A) net photosynthetic rate (Pn); (B) transpiration rate (E); (C) stomatal conductance (Gs); and (D) intercellular CO₂ concentration (Ci). These photosynthetic parameters were measured under white, blue, red, green, and yellow light for about 5 min each. Values are means of 5 replicates $\pm$ SD. Different letters (a, b, c, d) in the same column indicate significant differences among treatments at $P \leq 0.05$ according to Duncan's new multiple range test. W: white light; B: blue light; G: green light; Y: yellow light; R: red light.

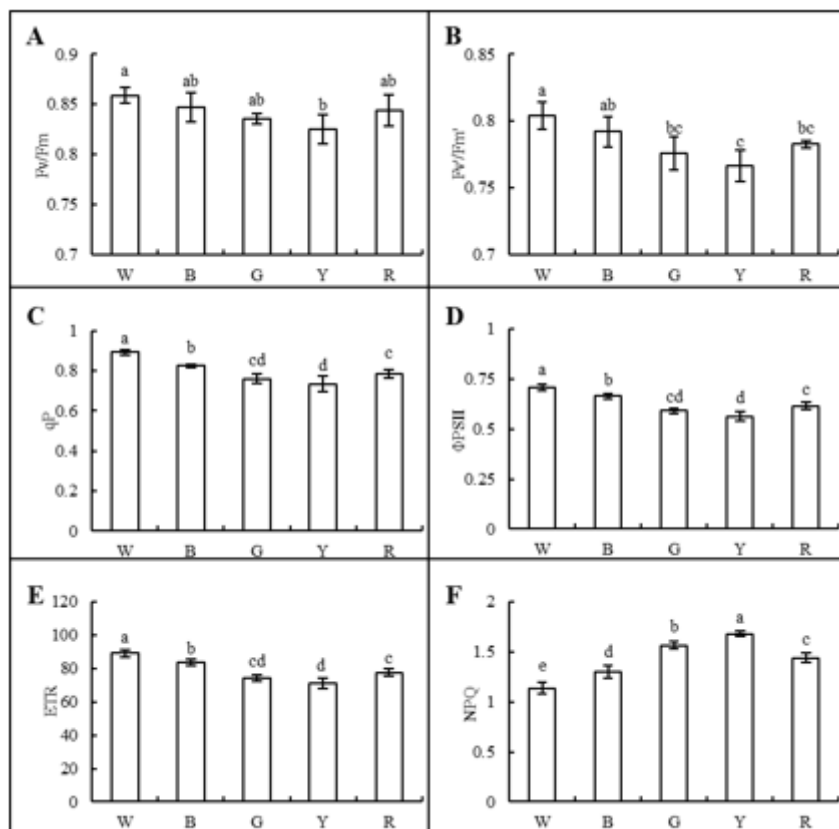


Figure 3

Responses of chlorophyll fluorescence parameters in Welsh onion to different LED light qualities, including: (A) maximum photochemical efficiency of PSII under dark adaptation (F_v/F_m); (B) maximum photochemical efficiency of PSII under light adaptation (F_v'/F_m'); (C) photochemical quenching coefficient (q_P); (D) actual photochemical efficiency (Φ_{PSII}); (E) apparent electron transport rate (ETR); and (F) non-photochemical quenching coefficient (NPQ) = $1 - (F_m' - F_o') / (F_m - F_o)$. Values are means of 5 replicates $\pm$ SD. Different letters (a, b, c, d) in the same column indicate significant differences among treatments at $P \leq 0.05$ according to Duncan's new multiple range test. W: white light; B: blue light; G: green light; Y: yellow light; R: red light.

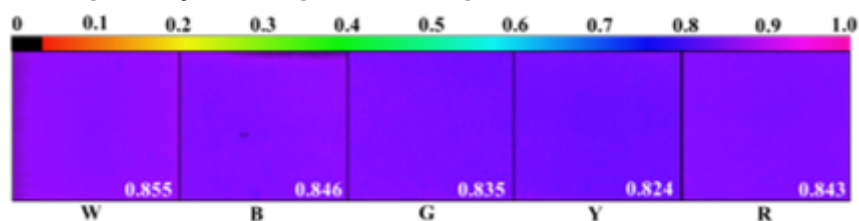


Figure 4

Chlorophyll fluorescence imaging analysis of Welsh onion leaves under different LED light qualities, including the maximum photochemical efficiency of PSII under dark adaptation (F_v/F_m) in them.

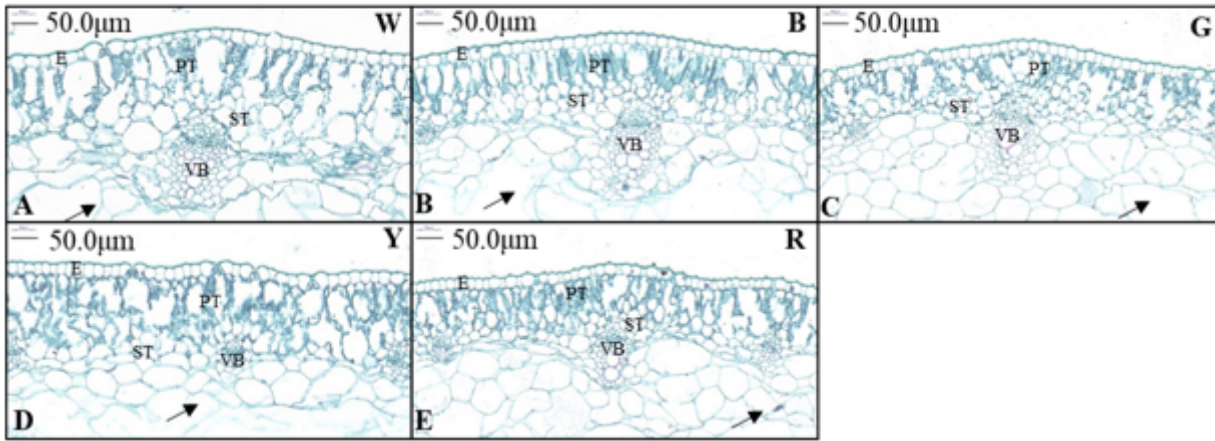


Figure 5

Responses of the leaf anatomy of Welsh onion to different LED light qualities. The fistular lamina of Welsh onion (*Allium fistulosum* L.) leaves changes from being solid to hollow during development, and the cells around the cavity break up until the remaining 1-2 layers of cells from the palisade layer show cell wall residues ('arrowheads') [26]. E: epidermis; PT: palisade tissue; ST: spongy tissue; VB: vascular bundle; W: white light; B: blue light; G: green light; Y: yellow light; R: red light. Scale bars = 50 μ m.

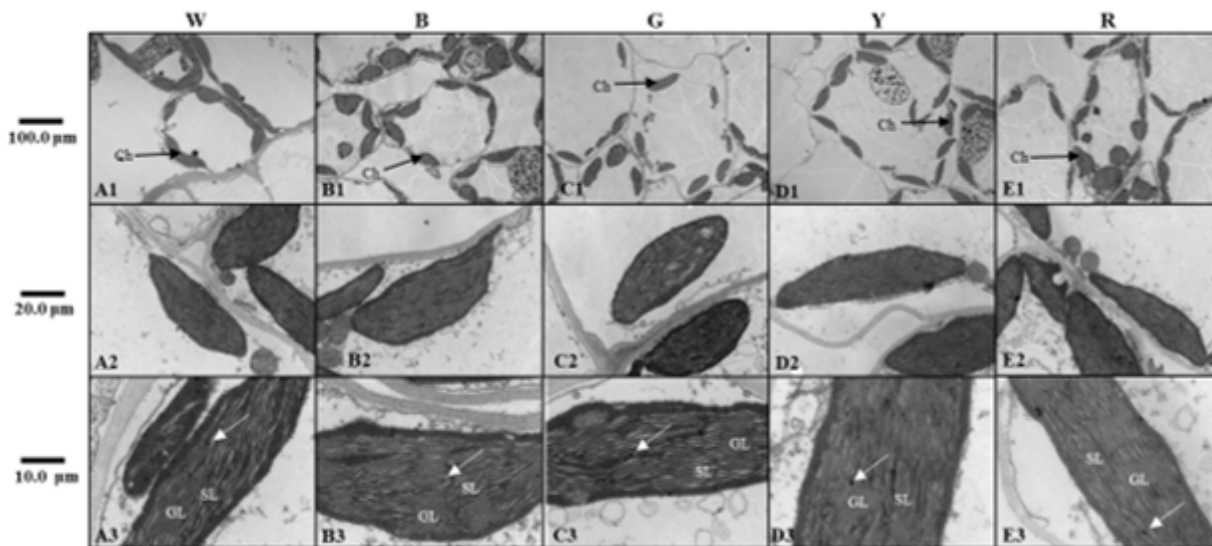


Figure 6

Responses of chloroplast ultrastructure in Welsh onion leaf cells to different LED light qualities. Ch: chloroplast; GL: grana lamella; SL: stroma lamella; white arrow: osmiophilic particles; W: white light; B: blue light; G: green light; Y: yellow light; R: red light.

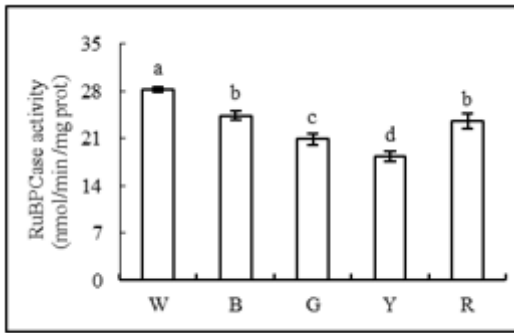


Figure 7

Responses of the RuBPCase activity in Welsh onion leaves to different LED light qualities. The ribulose-1,5-bisphosphate carboxylase (RuBPCase) activity of RuBisCo was determined using an ELISA kit (Suzhou Keming). Values are means of 5 replicates $\pm$ SD. Different letters (a, b, c, d) in the same column indicate significant differences among treatments at $P \leq 0.05$ according to Duncan's new multiple range test. W: white light; B: blue light; G: green light; Y: yellow light; R: red light.