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# Green light promotes healing and root regeneration in double-root-cutting grafted tomato seedlings

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ABSTRACT

Double-root-cutting (DRC) grafting is a new grafting method that makes it possible to ship grafted seedlings without using plug trays, through cutting off the roots of both scion and rootstock. However, graft healing and root regeneration are the two important factors determining the survival of the DRC grafted plants. Recent studies have shown that green light plays a crucial role in plant growth and development. We hypothesized that green light could stimulate the graft healing and root regeneration of the rootstock in DRC grafted seedlings. To test this hypothesis, we used tomato seedlings (*Solanum lycopersicum* cv. Beaded Curtain grafted on cv. Rootstock No. 1) exposed to white LED lamp (W) as a control (CK). In the treatment group, green light (10, 20 and 30%) was added to the red and blue spectrum without changing the intensity of red and blue fractions. The effects of different light qualities on graft union formation, survival rate, rooting of the rootstock hypocotyls, activities of antioxidant enzymes, chlorophyll content and grafted seedling quality of grafted tomato seedlings were then studied. Compared with DRC grafted seedlings exposed to the same light intensity, addition of 30% green light to red and blue lights increased the activities of antioxidant enzymes, chlorophyll content, plant height and index of seedling strength of grafted seedlings, showed a more positive effect on the development and performance of grafted seedlings, and promoted graft union, rootstock rooting and grafted seedling growth. Increasing the proportion of green light brought about better graft union and rootstock rooting. Our results showed that green light may reduce the degree of stomatal opening and transpiration rate during the early stages of grafting. Green light increased the activity of antioxidant enzymes, which was enhanced tissue lignification. Photosynthesis was driven by green light, which improved the development of aboveground parts, enhanced the transport of auxin from leaves to rooting zone, and promoted hypocotyl rooting of DRC grafted tomato seedlings.

## 1. Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most important horticultural crops in the world. China has the largest area of tomato cultivation and ranks first in the world in tomato production (FAO, 2020). To obtain high crop yield, Chinese farmers tend to grow tomatoes in long seasons (autumn to next summer) in solar greenhouses. However, tomatoes are often subjected to various biotic (such as extreme temperature and salinity) and biotic (e.g., soil-borne pathogens and nematodes, Lee et al., 2010) stress during such a long cultivation period, especially in a solar greenhouse. One way to improve plant resistance to biotic and/or abiotic stress is grafting (Lee et al., 2010). Compared with conventional grafting, double-root cutting (DRC) grafting has the advantages of faster grafting speed, higher survival rate and better hypocotyl rooting of rootstocks (Sun et al., 2020). DRC grafting can reduce the propagation time, and enhance plant vigor and productivity (Miceli et al., 2014).

Graft healing is the key factor determining the survival of DRC graft, which depends on complex interactions between the scion and rootstock cells (Melnyk and Meyerowitz, 2015). Graft union includes initial adhesion, production of the callus, formation of secondary plasmodesmata and differentiation of vascular bundles. Establishment of vascular bundles in the graft interface is considered as an indicator of successful graft union (Turquois and Malone, 1996; Yang et al., 2016). Grafting can generate excessive reactive oxygen species (ROS), leading to lipid peroxidation (Wang et al., 2007). As antioxidants in plants, superoxide

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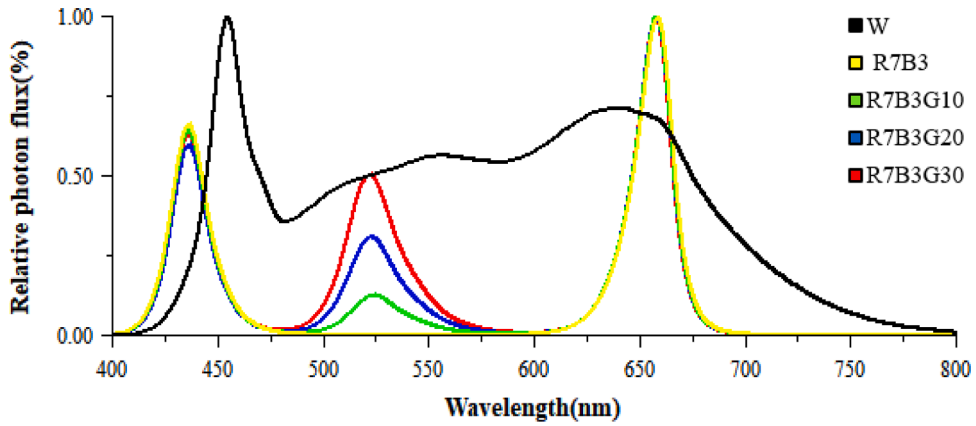


**Fig. 1.** The relative spectral distribution of white light, red-blue light and different proportions of red-blue-green light used in this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) can effectively scavenge harmful ROS produced after grafting, thereby preventing membrane system peroxidation and cell damage (Giannopolitis and Ries, 1977a, b). Thus, these antioxidants maintain the balance of ROS metabolism and protect membrane structure, and play an important role in the process of xylem differentiation at the grafting interface (Fernández-García et al., 2004).

Light is an important environmental factor influencing graft union (Lee et al., 2016). Green light has been reported to contribute to growth much less efficiently than other components of the visible spectrum (Smith et al., 2017). However, recent studies showed that green light also plays an important role in plant growth and development (Folta and Maruhnich, 2007; Johkan et al., 2012; Kaiser et al., 2019). Adding green light to red and blue has been reported to increase the activities of SOD, POD and CAT in the leaves of *Cunninghamia lanceolata* and improve the scavenging efficiency of ROS (Xu et al., 2019). Green light has been shown to support proliferation of calli and connection of vascular bundles at the interface between rootstock and scion during the early stages of grafting, and promotes the graft union formation (Mo et al., 2017). In addition, green light can reverse the effects of red and blue lights on plant growth and development, affect chlorophyll concentration by triggering the expression of the related genes, reduce stomatal opening, improve water use efficiency and mesophyll conductance (referring to the diffusivity of $CO_2$ in mesophyll cells) under short-term water stress, and support higher photosynthetic capacity (Bian et al., 2019).

In addition to graft healing, root regeneration is another important factor determining the success of DRC grafting. It was found that controlling light intensity/photoperiod could promote root regeneration from the rootstock hypocotyls and enhance graft union in DRC grafted seedlings (Sun et al., 2020). Light quality also plays a key role in regulating root formation, root performance and root secondary metabolism (Zhou et al., 2020). In an in vitro culture of cherry, it was found that a combination of red and blue (RB) could promote the induction of adventitious roots and root elongation (Iacona and Muleo, 2010). Shin et al. (2008) pointed out that red and blue light promoted the root growth and increased the leaf area of *Doritaenopsis* seedlings developed from tissue culture. Niemi et al. (2005) showed that different light combinations had significant effects on the development and formation of adventitious roots in *Pinus sylvestris* L. The R/B light combinations induced graft union and root biomass production in watermelon (Bantis et al., 2019). Red light promoted the production of adventitious roots and secondary metabolites in *Hypericum perforatum* detached leaves (Najafabadi et al., 2019). Red-rich light was found to enhance the transport of carbohydrates to the base of the stem, thus promoting rooting (Britz et al., 1985; Holzapfel et al., 1983; Saebo et al., 1995). Blue light has been reported to promote root formation in *Chrysanthemum* plants and increase the rooting rate and root numbers of *Achillea millefolium* culture and *Vanilla planifolia* plantlets (Ivan et al., 2015; Kurilčik et al., 2008; Ramírez-Mosqueda et al., 2017). Addition of green light to red, blue and purple lights was shown to enhance rooting, improve the root functions and antioxidant enzyme activity in *Cunninghamia lanceolata*, and root growth parameters are closely related to antioxidant capacity (Xu et al., 2019). Adding green light or partially replacing other spectra with it resulted in an increased biomass production of tomato and *ocimum basilicum* L. (Kaiser et al., 2019; Schenkels et al., 2019). Because the spectra of red and blue lights are similar to those required for plant photosynthesis, most studies have focused on evaluating the effects of monochrome or mixed red and blue lights. However, the effect of green light on tomato grafting has not yet been reported, especially in DRC grafted plants.

The effects of adding green light on plant has been reported extensively, however, most studies on green light have focused on physiological processes, growth, and development. Little information is available on the effects of green light on DRC grafting. We hypothesized that partial replacement of red and blue with green light could increase the activities of antioxidant enzymes and photosynthesis of DRC grafted tomato seedlings, which may enhance graft union and root regeneration. Thus, the aims of this study were to identify the effects of green light addition on the survival rate, graft union formation, rootstock root regeneration, chlorophyll concentration and quality of DRC grafted seedlings of tomato, and to specify the most effective light composition.

## 2. Materials and methods

### 2.1. Plant materials and growth conditions

Tomato varieties 'Beaded Curtain' and 'Rootstock No. 1′ (Henan Yuyi Seed Industry Co. Ltd, China) were used as scions and rootstocks, respectively. The scion seeds were sown two days after rootstock seeds. The scion seeds were sown in a hole-tray (50 holes, 4.8 × 4.8 cm), filled with a mixture of peat, vermiculite and perlite in the ratio of 2:1:1 (*v/v/v*). One week after sowing, water-soluble quick acting compound fertilizer (20–20–20+TE, N-P-K) was added twice a week (Beijing Dahan Landscape Co., Ltd.).

The scion and rootstock plants were used for DRC grafting when both produced three leaves (Lee and Oda, 2003). A 60°-cut was made at 1 cm above the cotyledons of the rootstock and the scion to ensure that the two incisions are identical, and the grafting ends were tightly fixed together with a transparent grafting tape. In order to obtain DRC grafted seedlings, the root of the rootstock was cut 4 cm below the cotyledons, and then inserted into a 50-hole tray with substrate, and the cutting depth was 1 cm. Each treatment included three replicates and each replicate had 50 grafted seedlings. The DRC grafted seedlings were transferred to an artificial climate chamber immediately after grafting,

watered on the eighth day after healing, and watered with nutrient solution every 7 days after survival. According to the actual production practice, the first 8 days of tomato grafting (0–24 h after grafting was the first day) were divided into four stages: 1–2 days (S1), 3–4 days (S2), 5–6 days (S3) and 7–8 days (S4). As from the first day after grafting, different light intensities were set in the stages described above. The light intensities of S1, S2, S3 and S4 were, respectively 50, 100, 150 and 200 μmol $m^{-2}$ $s^{-1}$ (Sun et al., 2020). The daytime/night temperature, light/dark time, relative humidity and carbon dioxide levels of the artificial climate room were 26/18 °C, 12/12 h, 80–95% and 800 μmol $mol^{-1}$ (Wang et al., 2016), respectively.

### 2.2. Light treatment

A LED lamp produced by Henan Zhishengpu Electronic Technology Co., Ltd. (China) was used as an auxiliary light source. According to the experimental requirements, the LED plant growth lamp (90 × 60 × 7 cm), rated voltage 220 V and rated power 15 W, was made. The light intensity was controlled by adjusting the current. The distance between the LED and seedlings was 50 cm. The range of supplementary light was 90 cm in length, 60 cm in width and 30 cm in height. The photon flux density (PPFD) and spectrum were measured with a spectrometer (Avaspec-ULS2048, Avantes, Apeldoorn, The Netherlands) at the vicinity of the seedling stem. The peak wavelengths of red LED (R), blue LED (B) and green LED (G) were 630 nm, 460 nm and 520 nm, respectively. Five light treatments based on different light combinations were used: white LED light (W) as a control (CK), and R/B of 7:3 (R7B3). In the treatment groups, red and blue light were replaced with 10, 20 and 30% green light (R7B3G10, R7B3G20 and R7B3G30), without changing the ratio of total light intensity to red and blue. The relative spectral radiation values of each light source are shown in Fig. 1.

### 2.3. Sampling and measuring methods

After 8 days in the healing chamber, the seedlings were moved to a solar greenhouse under minimum night temperature of 20 °C. On the second, fourth, sixth, eighth and tenth day after grafting, the grafted seedlings were randomly sampled for further analyses. Twelve grafted seedlings were collected from each treatment for each time point. Each treatment had three replicates and each replicate included four grafted seedlings.

#### 2.3.1. The survival rate and anatomical structure

The survival rate (SR) was calculated as follows (Temperini et al., 2013):

$$SR = (N2 / N1) \times 100\% \quad (1)$$

Where N2 is the surviving number of grafted seedlings at time T2 (after treatment), and N1 is the total number of grafted seedlings at time T1 (before treatment).

Samples of DRC grafted seedlings were collected at 2, 4, 6 and 8 days after grafting, and the anatomical structure of the grafting point during healing was investigated. The samples were fixed, dehydrated, infiltrated, and then embedded in paraffin according to Yang et al. (2016). The embedded samples were sectioned into 10 μm-thick cross sections with a rotary slicer, and then de-waxed and rehydrated. For optical microscopic observation, the sections were stained with 1% toluidine blue (Yang et al., 2016).

#### 2.3.2. Antioxidant enzyme activities

Samples of 0.2 g (about 2 cm graft segment) were ground with 0.2 mL phosphate buffer (pH 7.8) into a homogenate. Then the samples were centrifuged at 15,000 × g and 4 °C for 10 min, and the supernatant was collected and used for enzyme activity determination. According to the method of Giannopolitis and Ries (1977), the SOD activity was determined by monitoring the inhibition of photochemical reduction of nitro blue tetrazolium (NBT), using the hydrolysis rate of hydrogen peroxide as an index. The changes in absorbance at wavelengths of 240 and 470 nm were measured to determine CAT and POD activities, respectively (Cakmak and Marschner, 1992). The rate of oxidation of ascorbic acid, measured as changes in absorbance at 290 nm was used to determine the APX activity (Nakano and Asada, 1981).

#### 2.3.3. Root morphology

Root morphology was analyzed by using a root scanner (Expression 4990, Epson, Long Beach, CA) combined with Win RHIZO software (Régent Instruments Inc., Canada) (Füllner et al., 2012). The related parameters (length, diameter, surface area, volume, and number of tips and bifurcations) of the root were measured automatically. The root diameter was divided into four grades, including: (I) very fine root (0–0.5 mm), (II) fine root (0.5–1.0 mm), (III) fibrous root (1.0–1.5 mm), (1.5–2.0 mm) and (IV) coarse root (> 2.0 mm).

#### 2.3.4. Root activity

Root activity was analyzed by using triphenyl tetrazolium chloride (TTC) method (Zhang et al., 2013). The 0.5 g-fresh root samples were soaked in a uniform mixture of 10 mL containing 0.4% (*w/w*) TTC and 0.1 M potassium dihydrogen phosphate buffer (pH 7.5) and stored in the dark at 37 °C for 2 h. Subsequently, 2 mL of 1 M $H_2SO_4$ was added to stop the reaction, and then 10 mL of ethyl acetate was added. The absorbance of the extract at 485 nm was measured by using UV–visible spectrophotometer (UV-1800). The root activity (mg $g^{-1}$ $h^{-1}$) was expressed based on TTC reduction intensity:

$$Rootactivity = (TRA / RFW) \times T \quad (2)$$

Where TRA is the TTC reduced amount (mg), RFW is the root fresh weight (g), T is the time (h).

#### 2.3.5. Morphological index

The plant height was measured with a transparent ruler from the aboveground root to the growth point, and the stem diameter was measured with a Vernier caliper at 1 cm below the cotyledon base of the grafted seedlings. Leaf area was measured with leaf area meter (LI-3100, USA). The fresh aboveground parts and roots were weighed, and the dry weight was measured after de-enzyme at 105 °C for 30 min and drying at 75 °C for 24 h. The root shoot ratio (RSR) was calculated as follows (Temperini et al., 2013):

$$RSR = SDW / RDW \quad (3)$$

Where SDW and RDW are shoot dry weight (g) and root dry weight (g), respectively. The formula for calculating the seedling quality index (SQI) was as follow:

$$SQI = (WU / WA + S / H) \times W \quad (4)$$

Where WU is the dry weight of the underground part (g), WA is the dry weight of the aboveground part (g), S is the stem diameter (mm), H is the plant height (m), W is the dry weight of the whole plant.

#### 2.3.6. Chlorophyll concentration

Chlorophyll concentration was determined in the second true leaf above the cotyledon. Leaf samples of 0.2 g were homogenized with 20 mL of a mixture of acetone and anhydrous ethanol (1:1). The absorbance of the extract at 663, 646 and 470 nm was determined by ultraviolet-visible spectrophotometer (UV-1800) (Lichtenthaler and Wellburn, 1983).

### 2.4. Statistical analysis

The experiment was replicated three times with a design of

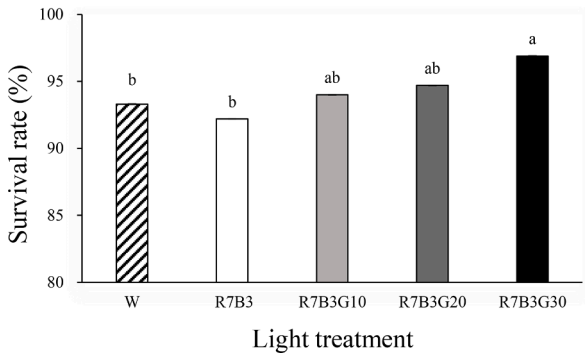


**Fig. 2.** Survival rate of tomato DRC seedlings incubated under different light qualities. Error bars represent the standard error, different small letters indicate significant differences at $p \leq 0.05$ by using Duncan's multiple range test.

randomized complete block ($n = 3$). The SPSS software v.22.0 (SPSS, Inc., Chicago, IL, United States) was used to analyze the data. The significant differences between treatments were determined by analysis of variance (ANOVA), Duncan multi-range test.

## 3. Results

### 3.1. The survival rate (SR) and anatomical structure of the graft union

The SR of tomato seedlings was maintained at a high level under all light treatments, where all treatments reached more than 90%, of which R7B3G30 was the highest, reaching 96.9%. The SR of R7B3 treatment was the lowest (92.2%), but there was no significant difference from W treatment. Addling green light significantly increased the SR of tomato DRC grafted plants, and effect that increased with increasing green light (Fig. 2).

Microscopic examination of the grafting interface showed that the healing process of graft was enhanced under green light as compared to the W and R7B3 lights (Fig. 3). On the second day after grafting, a thin and deep isolation layer was observed under the green light treatments of 10, 20 and 30%, and a small amount of callus was produced (Fig. 3 C2, D2 and E2). However, there was still a gap between the rootstock and the scion at the grafting site in the W and R7B3 treatments (Fig. 3A2,

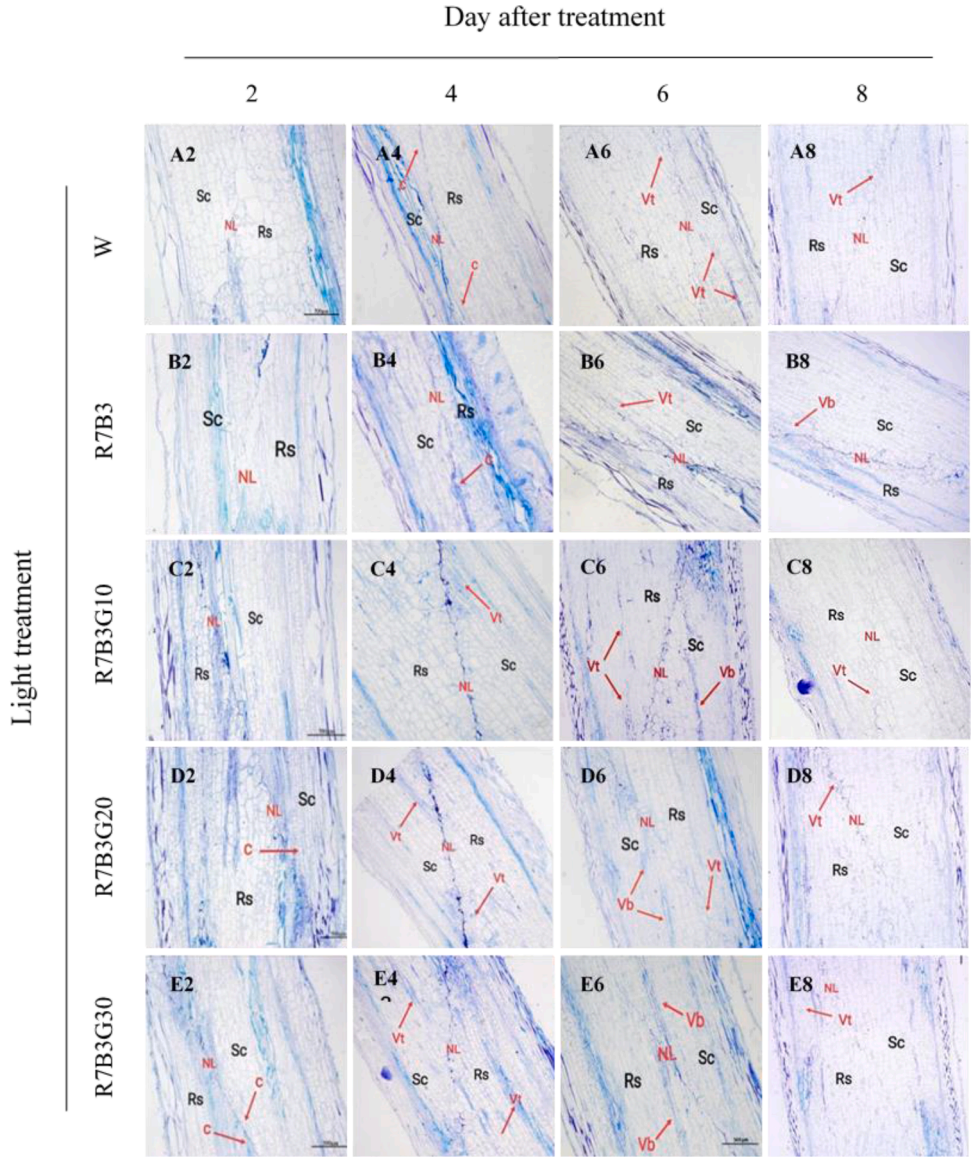


**Fig. 3.** Longitudinal sections of DRC grafted tomato seedlings after 2, 4, 6, 8 days of treatment with different light qualities, W (A), R7B3 (B), R7B3G10 (C), R7B3G20 (D), R7B3G30 (E). Rs: Rootstock; Sc: Scion; c: callus cell; NL: Necrotic layer; Vt: Vascular tissue; Vb: Vascular bridge.

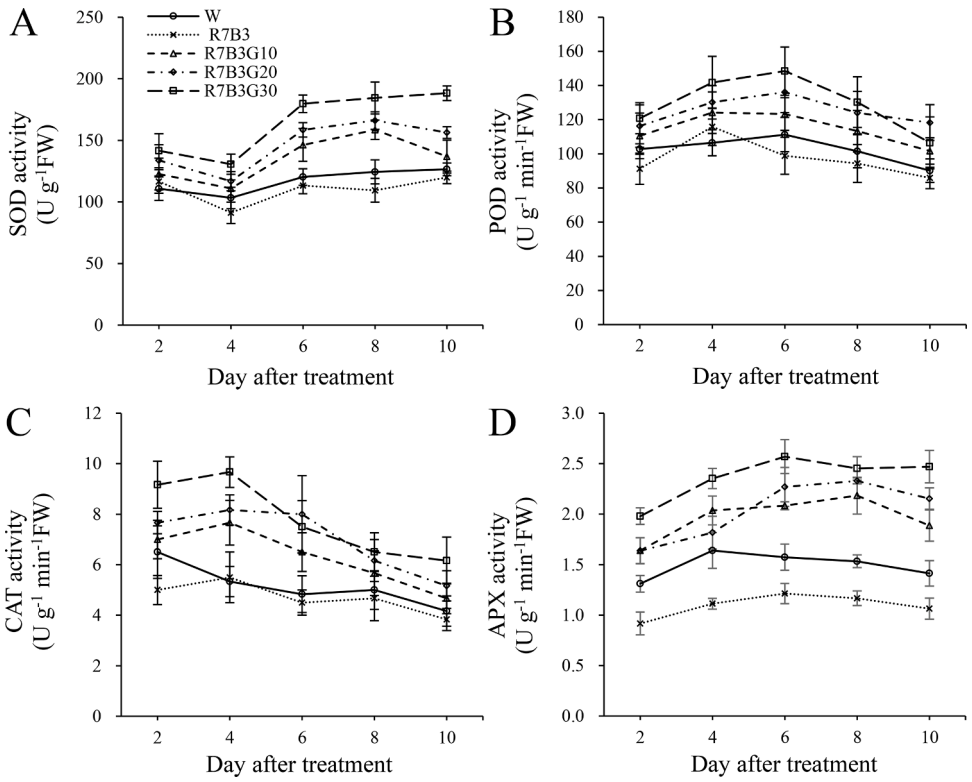


**Fig. 4.** Changes in SOD (A), POD (B), CAT (C), APX (D) activities of graft segment after 2, 4, 6, 8 and 10 days of treatment with different light qualities. The vertical bars represent the standard errors of the means.

B2). On the fourth day of healing, for the grafted seedlings treated with R7B3G20 and R7B3G30, the size of callus cells was almost equal on both sides of the scion, a large number of callus cells differentiated and proliferated, and some callus cells broke through the isolation layer and began to come into contact with each other (Fig. 3D4). Two or three layers of callus cells were produced at the interface of grafted seedlings treated with W and R7B3 light (Fig. 3A4, B4). On the sixth day of healing, along with the formation of the rootstock-scion callus, callus cells staggered in growth and combined into a cohesive mass. The isolation layers were further attenuated by R7B3G20 and R7B3G30 (Fig. 3D6, E6). The grafted seedlings of other treatments showed obvious cambium at the junction, and the callus cells continued to divide and their volume increased (Fig. 3 A6, B6 and C6). On the eighth day of healing, the vascular bundles of grafts treated with green light were completely connected, and the rootstock and scion were entirely rejoined (Fig. 3 C8, D8 and E8). There was also a lighter isolation layer at the joints treated with R7B3 (Fig. 3B).

### 3.2. Antioxidant enzyme activity

The SOD activity at the interface of DRC grafted seedlings initially decreased and then increased in all treatments. The treatment of R7B3G10 and R7B3G30 showed maximum SOD activities at 8 days after grafting, and addition of green light significantly increased the SOD activity. At 10 days after grafting, the SOD activity of R7B3G30 treatment was highest, where it was 56.9% higher than that of the lowest treatment (R7B3) (Fig. 4A).

The activities of POD and APX of DRC grafted seedlings showed an initial increase but then decreased. Treatment with green light increased the activities of POD and APX significantly, but then decreased both enzyme activities slowly. The POD activity in R7B3 treatment reached a maximum on the fourth day after grafting, but the other treatments did on the sixth day after grafting. On the sixth day after grafting, the POD activity of R7B3G30 treatment was highest, where it was 50.3% higher than that of control W, and there was no significant difference between R7B3G10 and R7B3G30 treatments. On the tenth day after grafting, the APX activity of R7B3G30 was significantly higher than that in other treatments, where it increased by 30.9 and 14.7% compared with R7B3G10 and R7B3G20 treatments, respectively (Fig. 4B, D).

At 10 days after grafting, except that CAT activity of W showed a downward trend, the CAT activity of other treatments increased at first and then decreased to a large extent. On the fourth day after grafting, the CAT activity of green light treatment was significantly higher than that of W and R7B3 treatments, and R7B3G30 was the highest (Fig. 4C). During the entire healing period after grafting, the activities of SOD, POD, CAT and APX of DRC grafted seedlings treated with green light

**Table 1**
The total root length (cm), root surface area ($cm^2$), root average diameter (mm), root volume ($cm^3$) and number of bifurcations in DRC grafted tomato seedlings after 10 days of different light quality treatments. Numbers are means ± standard errors of three repeats. Different small letters indicate significant differences between treatments at $p \leq 0.05$ by using Duncan's multiple range test.

| Treatment | Total root length (cm) | Root surface area weight ($cm^2$) | Root average diameter (mm) | Root volume ($cm^3$) | Number of bifurcations |
|---|---|---|---|---|---|
| W | 136.17 ± 4.62 c | 22.82 ± 2.08 c | 0.561 ± 0.048 a | 0.314 ± 0.029 bc | 2190 ± 117 bc |
| R7B3 | 104.18 ± 3.26 d | 21.98 ± 1.62 c | 0.464 ± 0.056 a | 0.262 ± 0.030 c | 1725 ± 84 c |
| R7B3G10 | 153.78 ± 3.48 bc | 33.46 ± 1.32 b | 0.485 ± 0.080 a | 0.420 ± 0.063 b | 2403 ± 372 bc |
| R7B3G20 | 171.55 ± 7.81 b | 39.78 ± 1.55 ab | 0.632 ± 0.070 a | 0.574 ± 0.056 a | 2887 ± 141 ab |
| R7B3G30 | 226.05 ± 9.20 a | 43.50 ± 3 0.64 a | 0.616 ± 0.046 a | 0.633 ± 0.041 a | 3197 ± 366 a |

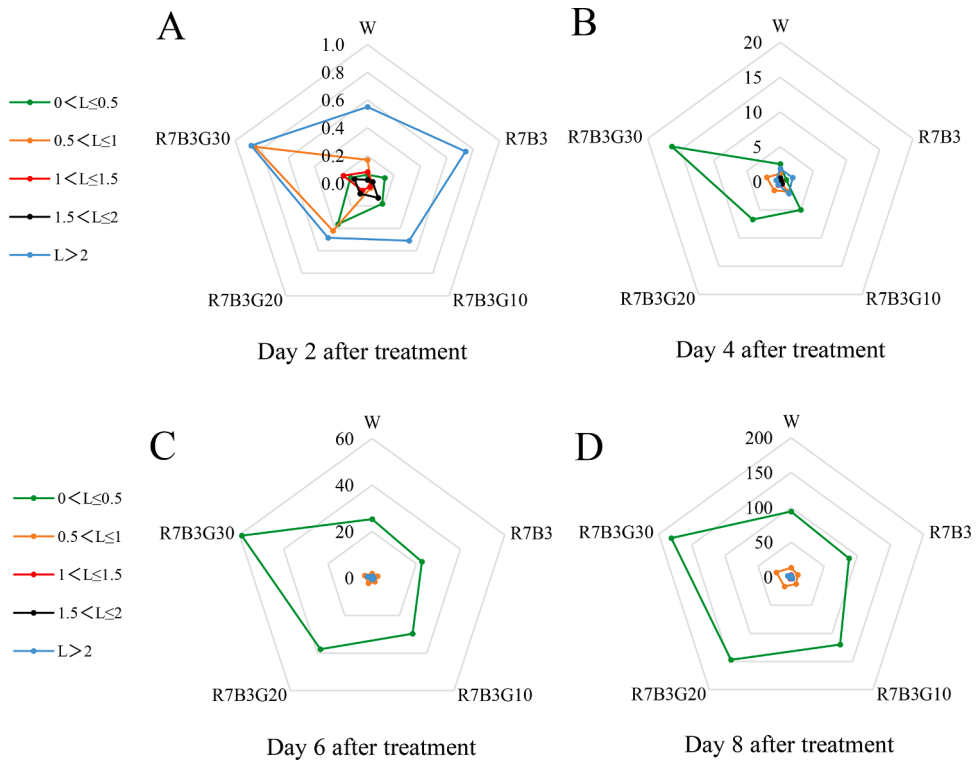


**Fig. 5.** Graded root length of DRC grafted tomato seedlings after 2 (A), 4 (B), 6 (C) and 8 (D) days of treatment with different light qualities, shown as radar maps.

were significantly higher than those of W and red-blue light treatments.

### 3.3. Root morphology

On the tenth day after grafting, the total root length of R7B3G30 was highest, where it was 66.0% higher than that of W treatment. The total root length of R7B3G20 and CK treatments was not significantly different from that of R7B3G10 treatment, but the total root length of R7B3 was significantly lower than that of W treatment. The root surface area, root volume and bifurcation number showed a similar trend, with the highest value in R7B3G30 and the lowest in R7B3. There was no significant difference in root average diameter among different treatments (Table 1).

On the second day after grafting, the new root of DRC grafted tomato seedlings was the root system with diameter more than 2.0 mm, and there were no significant differences among the treatments, where the leaves wilted slightly (Figs. 5A and 6). On the fourth day after grafting, the diameter of regenerated roots was 0–0.5 mm, and the number of roots with 0.5–1.0 mm diameter also increased greatly (Fig. 5B). There were no significant differences among the treatments with green light, which were higher than that of R7B3 and W treatments. On the sixth and eighth day after grafting, the number of 0–0.5 mm and 0.5–1.0 mm diameter regenerated roots increased rapidly. With the increase of the proportion of green light, the number of regenerated fibrous roots increased, and there were significant differences among different treatments. With the increase of healing days, the grafted seedlings in all treatments returned to the state of growth before grafting (Figs. 5C, D and 6).

### 3.4. Root tip number and root activity

There were significant differences in root tip growth rate in the regenerated roots of DRC grafted seedlings under different light treatments. The number of root tips in R7B3 treatment was significantly lower than that in other treatments. The root tip number in each treatment, on the fourth day, was significantly higher than that on the second day. The root tip number in R7B3G30 treatment was highest, where it was significantly higher than that of other treatments. On the sixth day after grafting, there was no significant difference between R7B3G10 and R7B3G20 treatments in terms of root tip numbers, which were higher than that of R7B3 and W treatments. On the eighth day after grafting, there were significant differences among treatments. Compared with W, R7B3, R7B3G10 and R7B3G20 treatments, the root tip number in R7B3G30 increased by 47.3, 53.7, 30.5 and 14.6%, respectively (Fig. 7A).

The root activity of each treatment increased with varying extents. On the second day after grafting, there were no significant differences among the treatments. On the fourth and sixth day after grafting, R7B3G20 and R7B3G30 treatments showed highest root activities, and there were no significant differences among other treatments. On the eighth day after grafting, R7B3G30 treatment had the highest root activity, which was 12.0, 12.0, 6.4 and 3.9% higher than that in W, R7B3, R7B3B10 and R7B3G20 treatments, respectively (Fig. 7B).

### 3.5. Morphological index

The leaf area, above-ground dry and fresh weights, root dry and fresh weights of the grafted seedlings were measured on the tenth day after grafting. The leaf area of the grafted seedlings in R7B3G30 treatment was highest. Except for R7B3 treatment was lowest, there were no significant differences in shoot fresh weight among other treatments. Green light significantly increased the biomass accumulation of tomato seedlings, where it brought about significant increase compared to the control W. The root dry and fresh weights of R7B3G30 treatment were the highest, and there were no significant differences among the treatments with green light (Table 2).

The RSR of DRC grafted seedlings showed an obvious increasing trend under different light quality treatments. R7B3 treatment had the lowest RSR in the whole experiment. On the second day after grafting, except for R7B3 treatment, there were no significant differences in RSR among other treatments. On the fourth day after grafting, there was no significant difference in RSR between R7B3G10 and R7B3G20

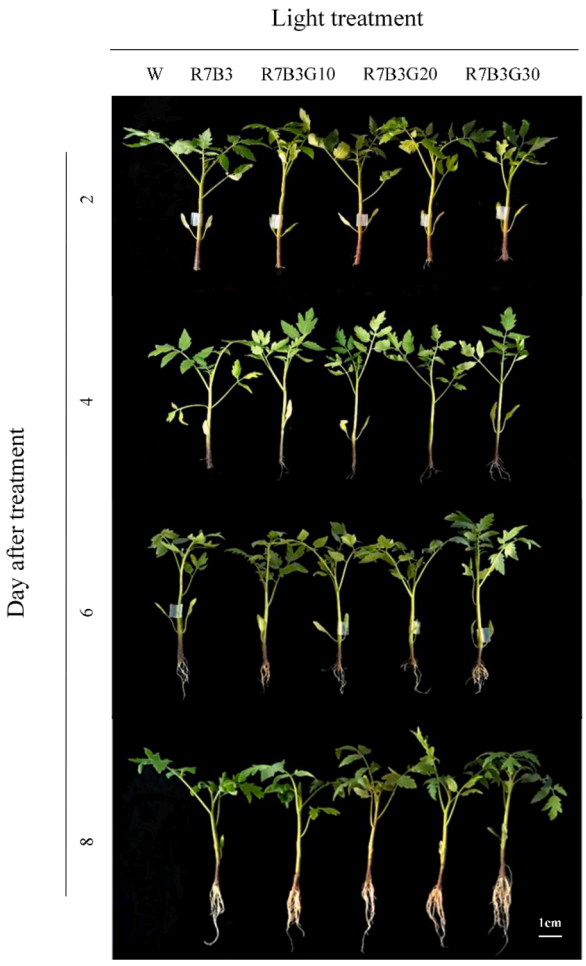


**Fig. 6.** Morphology of DRC grafted tomato plants after 2, 4, 6 and 8 days of treatment with different light qualities. Scale bars = 1 cm.

treatments, but there were significant differences among other treatments. The RSR of DRC grafted seedlings increased upon adding green light, where the RSR of R7B3G30 treatment was 117.1, 322.2, 58.3 and 35.7% higher than that of W, R7B3, R7B3G10 and R7B3G20 treatments, respectively. On the sixth and eighth day after grafting, the root/shoot ratio of 20 and 30% green light treatments showed no significant differences, but were higher than that of R7B3G10 and significantly higher than that of W and R7B3 treatments (Fig. 8A). Compared with the RSR, the growth rate of SQI (Fig. 8B), plant height (Fig. 8C) and stem diameter (Fig. 8D) of DRC grafted seedlings were relatively lower. On the second and fourth day after grafting, there were no significant differences in SQI among different treatments. Upon increasing days after grafting, the SQI of the green light treatments increased rapidly. On the eighth day after grafting, the SQI of R7B3G30 treatment was the highest, where increased by 23.9, 31.3, 15.9 and 11.3% compared with W, R7B3, R7B3G10 and R7B3G20 treatments, respectively. The increasing trend of plant height and stem diameter in different treatments was consistent with the SQI. On the second day after grafting, there were no significant differences in plant height and stem diameter among different treatments. On the sixth and eighth day of healing, the plant height and stem diameter in R7B3G30 treatment were the highest, which were significantly higher than those of W and R7B3 treatments.

### 3.6. Chlorophyll concentration

Under different light quality treatments, the concentration of total chlorophyll of DRC grafted seedlings increased with increasing the treatment time, whereas the concentration of chlorophyll b and carotenoids decreased initially and then increased. The chlorophyll a concentration in R7B3 was lower than that in other treatments on the fourth, sixth and eighth day after grafting, but there were no significant differences among R7B3B10, R7B3G20 and R7B3G30 treatments (Fig. 9A). There were no significant differences in chlorophyll b and carotenoid concentrations among the treatments on the second, fourth and sixth day after grafting, but its concentration in R7B3 was significantly lower than that of other treatments on the eighth day (Fig. 9B, C). The total chlorophyll concentration in W and R7B3 treatments

**Table 2**
Leaf area ($cm^2$), shoot fresh weight (g), root fresh weight (g), shoot dry weight (g) and root dry weight (g) of DRC grafted tomato seedlings after 10 days of different light quality treatments. Numbers are means ± standard errors of three repeats. Different small letters indicate significant differences between treatments at $p \leq 0.05$ by using Duncan's multiple range test.

| Treatment | Leaf area ($cm^2$) | Shoot fresh weight (g) | Root fresh weight (g) | Shoot dry weight (g) | Root dry weight (g) |
|---|---|---|---|---|---|
| W | 70.56 ± 2.36 bc | 3.65 ± 0.11 ab | 0.52 ± 0.059 bc | 0.33 ± 0.005 bc | 0.022 ± 0.004 bc |
| R7B3 | 68.03 ± 2.09 c | 3.35 ± 0.24 b | 0.42 ± 0.051 c | 0.31 ± 0.005 c | 0.017 ± 0.002 c |
| R7B3G10 | 74.28 ± 2.57 abc | 3.69 ± 0.05 ab | 0.61 ± 0.041 bc | 0.34 ± 0.009 bc | 0.030 ± 0.003 ab |
| R7B3G20 | 76.14 ± 2.01 ab | 3.70 ± 0.16 ab | 0.69 ± 0.055 ab | 0.35 ± 0.007 b | 0.031 ± 0.001 ab |
| R7B3G30 | 80.83 ± 2.48 a | 4.11 ± 0.02 a | 0.84 ± 0.046 a | 0.40 ± 0.010 a | 0.038 ± 0.002 a |

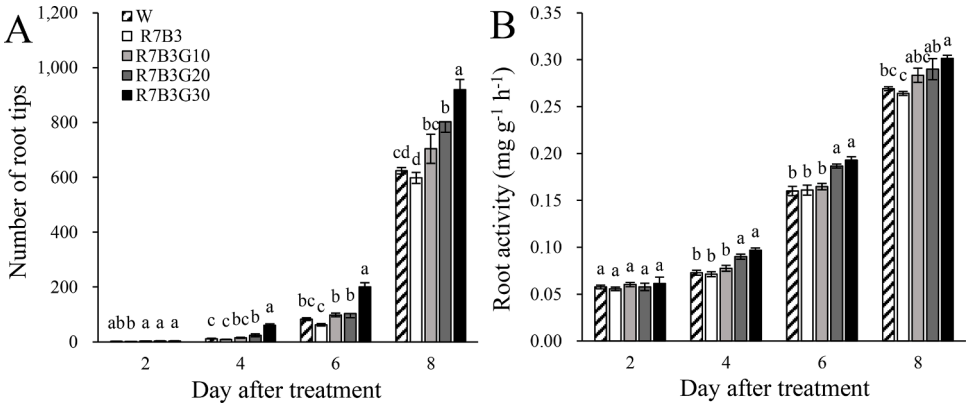


**Fig. 7.** The root tip numbers (A) and root activity (B) of DRC grafted tomato seedlings after 2, 4, 6 and 8 days of treatment with different light qualities. Error bars represent the standard error, different small letters indicate significant differences at $p \leq 0.05$ by using Duncan's multiple range test.

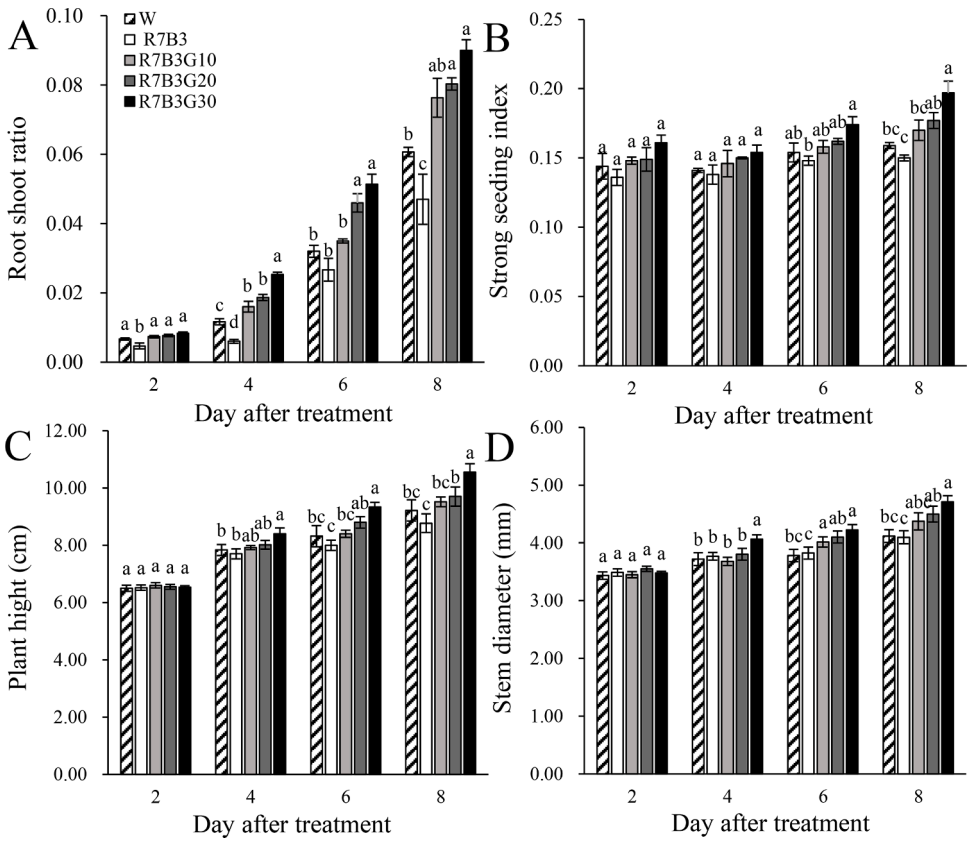


**Fig. 8.** The root shoot ratio (A), seedling quality index (B), plant height (C) and stem diameter (D) of DRC grafted tomato seedlings after 2, 4, 6 and 8 days of different light quality treatments. Error bars represent the standard error, different small letters indicate significant differences at $p \leq 0.05$ by using Duncan's multiple range test.

decreased initially but then increased, where it reached the lowest level on the fourth day. Addition of green light resulted in increasing the total chlorophyll concentration on the eighth day where such increase depended on the proportion of green light. On the eighth day after grafting, there were no significant differences in total chlorophyll concentration among the treatments with green light, which were higher than those in R/B and W treatments. The R7B3G30 treatment had the highest chlorophyll content where it was 16.6, 26.4, 9.9 and 3.9% higher than those in W, R7B3, R7B3G10 and R7B3G20 treatments, respectively (Fig. 9D).

## 4. Discussion

Previous studies have shown that light quality contributes to the developing connection of the vascular bundles as well as function to maintain the water status of the grafted seedlings (Lee et al., 2016). In the process of graft union, a firm contact of the graft tissues of root and scion stem is established, and the parenchyma cells begin to regenerate to interlock. Then there is the phase of cell differentiation, which involves the production of a large number of vessel cells and formation of the vascular bundle bridge. At last, the rootstock-scion callus begins to seal the gap, and the isolation layers gradually disappear forming a new convex layer between the callus bridges (Fernández-García et al., 2004; Yang et al., 2016). In this study, green light added to red and blue effectively promoted the healing of DRC grafting. Moreover, the healing rate of DRC grafted seedlings with 30% green light was fastest, and the isolation layer at the interface of rootstock and scion disappeared earliest compared to other light treatments (Fig. 3). A high frequency of callus formation was reported as essential for survival of grafted plants. Consequently, our results demonstrated that green light was beneficial to graft union and improved the SR of grafted plants (Fig. 2). A possible explanation for this result is that green light may decrease the stomatal aperture in leaves of grafted seedlings at the initial stages of grafting, leading to avoidance of excessive water loss from plant leaves, and enhancing the development and function of the vascular connections. This view is also supported by the study of Bian et al. (2019), who found that the reduced water loss from plant leaves as a consequence of green light resulted from early stomatal aperture reduction. To maintain the water status of grafted plants, stomatal functioning also plays an important role in the transport of ABA through xylem from the rootstock, where the developing xylem connections in the graft unions can be indicated by the avoidance of a higher transpiration rate of grafted seedlings under low leaf water potentials (Dodd et al., 2009). Lee et al. (2016) have reported that, vascular bundle connections and stomatal function were similarly reflected by the developing xylem connections.

The production of ROS is an important factor leading to physiological changes in grafted tomato seedlings, including changes in plant height and hardness of grafted joints and biomass. It is well known that SOD decomposes ROS into $H_2O_2$ and $O_2$. The enzymes POD, CAT and APX scavenge $H_2O_2$ from the peroxisomes and cytoplasm to maintain the balance of active oxygen metabolism in plants, so that plants can minimize or resist the mechanical damage caused by grafting at least partially. In this study, the antioxidant enzyme activities of grafted seedlings under all light treatments showed an increasing trend. Nevertheless, the activities of SOD (Fig. 4A), POD (Fig. 4B), CAT (Fig. 4C) and APX (Fig. 4D) in DRC grafted seedlings treated with red, blue and green light were significantly higher than in those treated with red and blue light and control. The results indicated that the addition of green light could improve the activity of antioxidant enzymes and reduce the lipid peroxidation induced by $H_2O_2$. Meanwhile, vascular regeneration involves the structural and physiological differentiation of parenchyma into xylem and phloem elements (Jeffree and Yeoman,

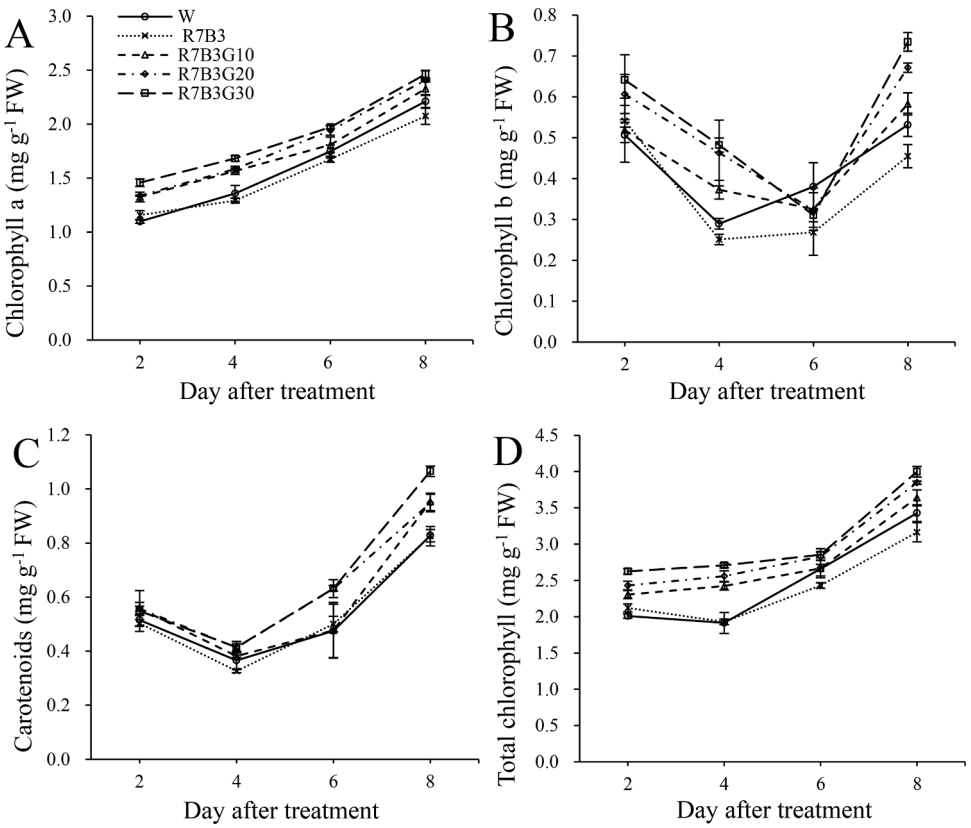


**Fig. 9.** Pigment concentrations in the second true leaves of DRC grafted tomato seedlings after 2, 4, 6 and 8 days of different light quality treatments. Values are leaf-area based concentrations of chlorophyll a (A), chlorophyll b (B), carotenoids (C) and total chlorophyll (D). The vertical bars represent the standard errors of the means.

1983). Deposition of lignin in plants is normally located in tracheary elements and fibers of the vascular tissues. The synthesis of lignin is catalyzed by POD (Whetten et al., 1998). Our work shows that the increase of POD activity was consistent with the process of vascular regeneration. The POD activity under green light treatment was significantly higher than that under other treatments (Fig. 4B), and the formation of vascular tissue was faster, which promoted the formation of new vascular bundles (Fig. 3) and improved the SR of the graft (Fig. 2). This result is consistent with the results of Fernández-García et al. (2004). Tissue printing of the grafted region demonstrated that POD was located mainly in the graft union area, and the increase of POD activity was consistent with the increase of lignification.

Our data support the hypothesis that green light can stimulate antioxidant enzyme activity and photosynthesis, thus promoting root regeneration of DRC grafted seedlings. The antioxidant enzyme systems make the plant environment relatively stable, promoting the photosynthesis and the translocation of photosynthates to the root, thus promoting the growth of the root system (Xu et al., 2019). The photosynthetic pigments are essential to photosynthesis. Light quality directly affects the synthesis of photosynthetic pigments, thus affecting plant photosynthesis (Tholen et al., 2007). Our data revealed that treatment with green light supported higher antioxidant enzyme activities (Fig. 4) and higher chlorophyll concentrations (Fig. 9). The grafted seedlings had higher root tip number, length, surface area, volume and root activity under R/B/G compound light (Table 1, Fig. 5), presumably due to the larger root absorption area and vigor of plants (Fig. 7), that increased the root absorptive capacity and promoted growth. The results showed that green light could increase the content of pigments in the leaves of grafted seedlings, promote the absorption of light energy, and further improve the efficiency of photosynthesis. This is consistent with previous studies which revealed that tomato leaves showed significant increases in the chlorophyll and carotenoid concentrations with increasing green light intensity (Kaiser et al., 2019). Similarly, Bian et al. (2018, 2019) found that green light accelerated the permeation of $CO_2$ from the intercellular spaces to the active site of Rubisco inside the chloroplasts to promote photosynthesis under drought stress. Light has been reported to stimulate the development of leaves and enhance auxin transport from leaves to the rooting zone, which promoted hypocotyl rooting in tomato seedling cuttings (Tyburski and Tretyn, 2004). On the other hand, it was found that root tip regeneration was related to the activity of the plant auxin indole acetic acid (IAA). Regeneration was reported to be initiated by the rapid accumulation of auxin near the injured site (Matosevich et al., 2020). Green light may promote the rapid accumulation of auxin, which further promotes the root regeneration of DRC grafted tomato seedlings.

Increasing the photosynthetic efficiency during healing and acclimatization was reported to improve growth and quality of grafted plants (Jang et al., 2011). Seedling quality reflects the extent to which a seedling may be expected to survive and grow after transplanting (Wilson and Jacobs, 2006). With the increase of the proportion of green light, the plant height, stem diameter, leaf area and SI of the grafted tomato seedlings also increased (Table 2 and Fig. 8). During the healing period, the chlorophyll concentration of the grafted seedlings treated with R7B3 and CK decreased initially and then increased, while treatment with green light showed an overall increasing trend. The concentrations of chlorophyll a and carotenoids in all treatments increased with increasing the green light (Fig. 9). Chlorophylls are basic structural and redox components of the light-harvesting complex of photosystems I and II; thus, their accumulation and allocation are indicative of the plant physiological status (Strasser et al., 2010). This result is consistent with previous studies, where partial replacement of blue and red light with green light resulted in a significant increase in biomass production in

*Ocimum basilicum* L. compared to plants grown under a control spectrum at equal light intensity (Schenkels et al., 2019). With increasing green light percentage, there were linear increases in leaf biomass, specific leaf area, stem biomass, stem length and internode number of tomato plants (Kaiser et al., 2019). The increased total leaf area could increase the level of photosynthesis of the whole plant and promote dry matter accumulation (Claypool and Lieth, 2020).

## 5. Conclusion

In tomato DRC grafting, the addition of green light to R/B light promoted the formation of graft union and rooting of hypocotyls of rootstocks. The addition of 30% green light improved the healing process of grafted seedlings, SR and quality of grafted seedlings, and promoted roots tock hypocotyl rooting. This study provides an improved protocol for the production of DRC grafted seedlings of tomato, although the specific mechanisms of the effects of green light on DRC grafted seedlings remains to be further studied. Light quality was reported to modulate its effects by regulating the gene expression of some functional proteins or enzymes, thus influencing the healing process of grafted seedlings, root growth and development (Szechynska-Hebda et al., 2010; Xu et al., 2016). As a result, the future research direction is to deeply understand the mechanism of gene regulation and protein expression during graft healing.

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## CRediT authorship contribution statement

**Fenghua Li:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Yang Li:** Formal analysis, Investigation, Writing – review & editing. **Shengli Li:** Conceptualization, Methodology, Formal analysis, Supervision, Funding acquisition. **Guoxiu Wu:** Methodology, Investigation, Formal analysis. **Xuxu Niu:** Investigation, Formal analysis. **Aimin Shen:** Methodology, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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