Regulation of Chloroplast Ultrastructure, Cross-section Anatomy of Leaves, and Morphology of Stomata of Cherry Tomato by Different Light Irradiations of Light-emitting Diodes

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Abstract. The chloroplast structural alteration and the photosynthetic apparatus activity of cherry tomato seedlings were investigated under dysprosium lamp [white light control (C)] and six light-emitting diode (LED) light treatments designated as red (R), blue (B), orange (O), green (G), red and blue (RB), and red, blue, and green (RBG) with the same photosynthetic photon flux density (PPFD) ($\approx 320 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for 30 days. Compared with C treatment, net photosynthesis of cherry tomato leaves was increased significantly under the light treatments of B, RB, and RBG and reduced under R, O, and G. Chloroplasts of the leaves under the RB treatment were rich in grana and starch granules. Moreover, chloroplasts in leaves under RB seemed to be a distinct boundary between granathylakoid and stromathylakoid. Granathylakoid under treatment B developed normally, but the chloroplasts had few starch granules. Chloroplasts under RBG were similar to those under C. Chloroplasts under R and G were relatively rich in starch granules. However, the distinction between granathylakoid and stromathylakoid under R and G was obscure. Chloroplasts under O were dysplastic. Palisade tissue cells in leaves under RB were especially well-developed and spongy tissue cells under the same treatment were localized in an orderly fashion. However, palisade and spongy tissue cells in leaves under R, O, and G were dysplastic. Stomatal numbers per mm^2 were significantly increased under B, RB, and RBG. The current results suggested blue light seemed to be an essential factor for the growth of cherry tomato plants.

Cherry tomato (*Solanum lycopersicum* Mill.) plants are one of the cultivars of tomato species and annual plants that prefer a high light fluence rate. The fruits of cherry tomato plants have pleasing appearances and a delicious taste and are well accepted by consumers. The photosynthesis and growth of the tomato plants are greatly influenced by the quality and quantity of light (Hiroshi et al., 2000; Kinet, 1977).

Nowadays, many kinds of garden crops are cultivated under electric lights such as fluorescent lamps and LEDs. LEDs are becoming especially popular for the cultivation of vegetable crops (Amaki and Hirai, 2008; Goins et al., 1997; Hoenecke et al., 1992; Kim et al.,

2004a, 2004b; Schuerger et al., 1997; Tennessen et al., 1994).

The quality and quantity of light have been shown to alter the structure and function of chloroplasts in leaves (Albertsson, 2001; Anderson, 1999; Danielsson et al., 2004). The alteration of photosynthesis activity and the structure of granathylakoids and stromathylakoids by the different light treatments is of particular interest (Danielsson et al., 2004; Mustardy and Garab, 2003).

Light quality influences the growth of cells and tissue, photosynthetic characteristics (Liu, 1993) and yield of crops, physiological and morphological qualities, and the regulation of stress and aging of leaves (Voskresenskaya et al., 1968). At present, photobiological studies have been mainly focused on the effects of ultraviolet radiation on physiological and morphological characteristics of plants (Holzinger et al., 2006; Holzinger and Lütz, 2006; Michael et al., 2009; Poppe et al., 2002; Zancana et al., 2008). Different treatments of blue, red, and far-red light have been used to analyze the ultrastructure of organelles in leaf

cells (McMahon and Kelly, 1996; Schuerger et al., 1997). However, few studies on the ultrastructure and response of cell organelles in leaves exposed to light of different spectral qualities have been carried out.

In the present experiment, we investigated the effects of dysprosium lamps (white light, control) and the respective light treatments of LEDs designated as red, blue, orange, green, red and blue, and red, blue and green on the photosynthesis of leaves, ultrastructure of chloroplasts, palisade/spongy tissue, and stomata of cherry tomato leaves.

Materials and Methods

Plant materials and culture conditions. Seedlings of cherry tomato (*Solanum lycopersicum* Mill.) (provided by Taiwan Farmers Co.), which developed two leaves after germination, were transplanted and grown in plastic pots containing a mixture of peat and vermiculite (3:1, v/v) under light treatments. The treatments were provided by a dysprosium lamp (It is a high-intensity gas discharge lamp, a new type of metal halide lamp. Its spectrum is similar to the solar spectrum.) (white light, C) (LZ400D/H, 400W; YaHuaNing Co., Nanjing, China) and LEDs designated as R, B, O, G, RB, and RBG. The RB combination of spectral energy distribution was shown to be R:B = 1:1. The RBG combination of spectral energy distribution was shown to be R:B:G = 3:3:1. Except for the power of green lamp in the RBG treatment, which was 3 W, the power of every LED lamp treatment was 9 W. The number of LED lamps in treatments of R, B, and RB was 10 each, whereas the numbers used in treatments O, G, and RBG were 12. Respective LEDs were operated with the same PPFD ($\approx 320 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for 30 d. Spectral distribution and total power for each treatment are shown in Figure 1 and Table 1. Seedlings were incubated at 28 °C in the daytime and at 18 °C at night; relative humidity (RH) was 60% $\approx$ 80%, and daylength of 12 h was used. The light system was designed and made by Nanjing Agricultural University.

Measurements of photosynthesis. All measurements were carried out using the young and fully expanded third leaf of cherry tomato plants. PPFD was measured using a quantum sensor (LI-250; LI-COR) and photosynthesis was measured using a photosynthesis instrument (LI-6400; LI-COR). PPFD was set to measure at $800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and the experimental conditions such as leaf temperature, CO_2 concentration, and RH were 23 ± 1 °C, $380 \pm 5 \mu\text{L}\cdot\text{L}^{-1}$, and 16% to 20%, respectively. Spectral distribution of light treatments was measured by spectroradiometer (OPT-2000; ABDPE Co., Beijing, China). Leaves of three plants per treatment were measured and repeated twice.

Chloroplast ultrastructure. Leaf samples were collected after illumination for ≈ 3 h at 30 d and placed into 0.2 M phosphate buffer (pH 7.2) containing 2.5% glutaraldehyde and then subjected to suction by a vacuum pump. After that, the samples were placed in a refrigerator at 4 °C for 8 h; they were washed

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three times with 0.2 M phosphate buffer (pH 7.0). The washed samples were fixed for 120 min with 1% osmic acid prepared with 0.2 M phosphate buffer (pH 7.2) and washed again with the same buffer (pH 7.0) three times. The resulting samples were finally washed with double-distilled water two times at intervals of 10 min. After the samples were washed with double-distilled water, they were dehydrated with ethanol twice each at 30%, 50%, 70%, 90%, and 100% and then soaked in epoxy propane and embedded with Epon-812 epoxy resin and allowed to polymerize the epoxy resin at 30 °C for 24 h, 40 °C for 24 h, and 60 °C for 48 h. The resulting samples were sectioned with an ultra-microtome (Power Tome-XL; RMC Inc.) and treated with uranyl acetate, then followed by lead citrate. The treated samples were observed and photographed with an electron microscope (H-7650; Hitachi Ltd, Tokyo, Japan).

Leaf anatomical analysis. The anatomical analysis of mesophyll cells in leaves of cherry tomato seedlings was carried out by the method of Yao et al. (2007). The anatomical structure of mesophyll cells of leaves was examined under a light microscope (DP71; OLYMPUS Inc., Tokyo, Japan). The thickness of palisade and spongy tissue of leaves was measured with a light microscope connected to an imaging analysis system.

Stomata analysis. Stomata of the leaf epidermis were analyzed according to Duan

et al. (2008). The light microscopy images were processed using a light microscope (DP71; OLYMPUS Inc.) connected to an imaging analysis system. The numbers of stomata per field of vision of leaf epidermis were converted to numbers/mm² (stomatal density). The space area (stoma) was measured using at least 32 stomata sampled randomly.

Statistical analysis. Data were analyzed using a multifactor analysis of variance. Differences among means were calculated using the least significant difference range test with a family error rate of 0.05 by using the statistical analysis software SAS 8.0 (SAS Institute Inc., Cary, NC). The variables were measured after 30 d under the described treatments.

Results

Net photosynthesis. Net photosynthesis (P_n) of cherry tomato leaves was shown to be significantly different under the different light treatments (Fig. 2). Compared with the white light control, P_n under the RB treatment was significantly increased and under B and RBG was increased, but not significantly. P_n was shown to be reduced under R, O, and G, but there was no significant difference with the G treatment.

Chloroplast ultrastructure. Ultrastructure of chloroplasts showed remarkable differences among light treatments (Fig. 3). Chloroplasts

in leaves irradiated with R had some large starch grains, and the lamellar structure between granathylakoids and stromathylakoids in the chloroplasts was shown to be unclear as compared with the control (Fig. 3). Chloroplasts in leaves irradiated with B contained few starch grains, and the lamellar structure between granathylakoids and stromathylakoids in the chloroplasts was relatively clear (Fig. 3). Moreover, the granathylakoids in these chloroplasts were shown to be dense and thick, whereas the stromathylakoids were sparse (Fig. 3). Chloroplasts in treatment O contained a few starch grains, and the boundary between granathylakoids and stromathylakoids was obscure and stroma in the chloroplasts was sparse (Fig. 3). Chloroplasts in leaves under G were shown to have more starch grains than those under C. Moreover, the boundary between granathylakoids and stromathylakoids under G was clearer than under O, but the number of grana in chloroplasts was clearly less than under B and RB (Fig. 3). Furthermore, mesophyll cells under RB contained significantly more chloroplasts than those under the other LED light treatments (data not shown). The chloroplasts under RB contained more starch grains. The boundary between granathylakoid and stromathylakoid in the chloroplasts was clearly distinguished and granathylakoid was shown to form several layers stacked densely and in an orderly pattern (Fig. 3). The chloroplasts under RBG contained more starch grains and the thylakoid structure was similar to C (Fig. 3). Chloroplast shape under R was similar to that under RB (Fig. 3), whereas there was similarity of shape among chloroplasts under the C, B, O, G, and RBG treatments. The character of shape is probably related to starch content in chloroplasts being thinner and longer when starch content is lower.

Palisade and spongy mesophyll cells. Palisade and spongy mesophyll cells of leaves under LED light treatments showed significant differences (Fig. 4; Table 2). Leaf thickness and length of palisade cells under R, O, and G treatments were significantly lower than those under the white light control. However, the proportion of spongy cells occupied among mesophyll cells in leaves was large; the

Fig. 1. Spectral distribution of light treatments (C = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs). Spectral distribution of RB (red and blue LEDs) and RBG (red, blue, and green LEDs) is, respectively, the combination of R and B and R, B, and G. PFD = photon flux density; LEDs = light-emitting diodes.

Table 1. Peak wavelength and total power of light treatments.

Variables	Light treatments ^a						
	C	R	B	O	G	RB	RBG
Emission peak wavelength (nm)	As shown in Figure 1	640	450	590	520	640 and 450	640, 450, and 520
PPFD (μmol·m ⁻² ·s ⁻¹)	320 ± 15	320 ± 15	320 ± 15	320 ± 15	320 ± 15	320 ± 15	320 ± 15
The number of lamps	1	10	10	12	12	5 and 5	4, 4, and 4
Power of each lamp (W)	400	9	9	9	9	9 and 9	9, 9, and 3
Total power (W)	400	90	90	108	108	90	84

^aC = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs; RB = red and blue LEDs; RBG = red, blue, and green LEDs.

PPFD = photosynthetic photon flux density; LEDs = light-emitting diodes.

Fig. 2. Effects of the different light treatments of LEDs on net photosynthesis of cherry tomato leaves. C = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs; RB = red and blue LEDs; RBG = red, blue, and green LEDs. Different letters indicate significant differences at $P < 0.05$. Error bars indicate the SD ($n = 6$). LEDs = light-emitting diodes

Fig. 3. Effects of the different light treatments of LEDs on structure of chloroplasts in cherry tomato leaves. C = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs; RB = red and blue LEDs; RBG = red, blue, and green LEDs. CW = cell wall; CP = chloroplast; SG = starch grain; G = granathylakoid; ST = stomathylakoid; LEDs = light-emitting diodes.

Fig. 4. Effects of the different light treatments of LEDs on anatomical structure of cherry tomato leaves. C = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs; RB = red and blue LEDs; RBG = red, blue, and green LEDs. PT = palisade tissue cells; ST = sponge tissue cells; UE = upper epidermis; LE = lower epidermis; S = stomata; LEDs = light-emitting diodes.

Table 2. Effects of the different light treatments on structure of cherry tomato leaves.

Light treatment ^a	Thickness of leaves (μm)	Length of palisade cells (μm)
C	34.103 b ^b	15.709 a
R	23.095 c	2.511 c
B	37.037 ab	14.943 a
O	20.979 c	5.900 b
G	23.022 c	8.535 b
RB	35.915 ab	14.437 a
RBG	39.736 a	17.811 a

^aC = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs; RB = red and blue LEDs; RBG = red, blue, and green LEDs. ^bDifferent letters indicate significant differences at $P < 0.05$ ($n = 9$). LEDs = light-emitting diodes.

palisade cells under the R and O treatments scarcely showed development (Fig. 4). Palisade cells under the G treatment showed better development as compared with those under O (Fig. 4). Leaf thickness under the respective treatments of B, RB, and particularly RBG was somewhat increased as compared with the control, particularly that under RBG (Table 2). The palisade cell length for leaves under the respective treatments of C, B, RB, and RBG showed no significant difference (Table 2). The palisade cells of leaves under the RB treatment were almost the same length, and spongy cells were well-developed (Fig. 4). The palisade cells under RBG and B also developed well, but the spongy mesophyll tended to become disorganized in plants grown under B and RBG (Fig. 4).

Stomata. The different treatments of LEDs also influenced the stomata of the leaf epidermis of tomato plants (Fig. 5). The diameters in length (a) of the stomata were increased under the respective treatments of R, B, O, RB, and RBG and reduced under G as compared with the control. The maximal influence was the result of the treatments with blue light (Table 3). Moreover, the diameters in width (b) of the stomata were increased under B, O, RB, and RBG, shown to be unaffected under R, and reduced under G. The area ($\pi ab/4$) of stomata opened under the respective treatments of R, B, and O was increased. However, under RB and RBG treatments, no effects were observed and under G, a reduction was observed (Table 3). The numbers of stomata/mm² were increased under B, G, RB, and RBG and unaffected by R and O (Table 3).

Discussion and Conclusion

Plant leaves are the main organ of photosynthesis. Structure and function of chloroplasts are important for the growth of plants and influence physiological and ecological responses (Peng and Zhou, 2009). Chloroplast development depends on light, and different wavelengths of light affect chloroplast structure and chemical changes in plants (Deng, 2007). Zhang et al. (2010) noted that chloroplasts in tomato leaves developed normally under the blue and red light, and lamella structure is stacked densely. Under yellow light (peak wavelength, 585 nm) treatment,

Fig. 5. Effects of the different light treatments of LEDs on stomata in lower epidermis of cherry tomato leaves (C = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs; RB = red and blue LEDs; RBG = red, blue, and green LEDs. S = stomata; E = epidermis; LEDs = light-emitting diodes. Scale bar is 25 μ m.

Table 3. Effects of the different light treatments on stomata in lower epidermis of cherry tomato leaves.

Light treatment ^z	Diam in length of stomata (a) (μ m)	Diam in width of stomata (b) (μ m)	Area of stomata ($\pi ab/4$) (μ m ²)	Number of stomata (number/mm ²)
C	7.635 bc ^y	5.527 ab	33.107 b	1799.6 c
R	8.456 ab	5.579 ab	37.077 ab	1656.4 c
B	9.436 a	6.050 a	44.769 a	2678.9 a
O	8.468 ab	5.100 a	39.887 ab	1717.8 c
G	6.618 c	4.730 b	24.593 c	2229.0 b
RB	8.087 abc	5.658 a	35.907 b	2658.5 a
RBG	7.864 abc	6.140 a	37.825 b	2413.1 ab

^zC = dysprosium lamp; R = red LEDs; B = blue LEDs; O = orange LEDs; G = green LEDs; RB = red and blue LEDs; RBG = red, blue, and green LEDs.

^yDifferent letters indicate significant differences at $P < 0.05$ ($n = 32$).

LEDs = light-emitting diodes.

grana are scattered and lamellae structure is vague. In our study, chloroplasts seem to show the best development under blue light treatments, B, RB, and RBG. Chloroplasts under R, O, and G showed obvious dysplasia, particularly those exposed to orange light (Fig. 3). Blue light is involved in a wide range of plant processes such as leaf photosynthetic functioning (Brown et al., 1995; Bukhov et al., 1995; Hogewoning et al., 2010; Matsuda et al., 2004, 2008; Ohashi-Kaneko et al., 2006; Whitlam and Halliday, 2007; Yorio et al., 2001). At the chloroplast level, blue light has been associated with the expression of “sun-type” characteristics such as a high photosynthetic capacity (Lichtenthaler et al., 1980). In our study, compared with the control, photosynthesis under R, O, and G was reduced. Photosynthesis under the respective blue light containing treatments of B, RB, and RBG was increased with the RB treatment showing maximal enhancement (Fig. 2). This result is probably because cryptochromes (CRYs) and phototropins are specifically sensitive to blue light, and phytochromes are specifically sensitive to red light (Whitlam and Halliday, 2007). Fankhauser and Chory (1997) reported that

very low fluences of blue light induced the expression of a nuclear photosynthesis gene, LHCB, in a phytochrome-dependent manner that was independent of CRY1. The expression of a number of chloroplast-encoded genes requires high irradiance blue light, suggesting that these genes are regulated by an additional receptor (Christopher and Mullet, 1994). Moreover, phytochrome affects photosynthesis by affecting chlorophyll content (Casal, 2000). The difference between RB and RBG is probably caused by green light antagonizing to some blue light responses such as stomatal opening (Folta and Maruhnich, 2007). The different results of light treatments between C and B, RB, and RBG, which all contain blue light, is probably caused by different spectral distributions of each blue source. As compared with the control, the G treatment photosynthetic rate is not significantly reduced, probably because the green light source has a significant blue component (Fig. 2). According to Tang and Shi (1997), the numbers of grana and the dense structure of lamella between granathylakoids are related to the capacity of photosynthesis. Tao et al. (1992) reported that the net photosynthetic rate of tomato leaves is closely

related to the lamella structure forming grana that are stacked densely and in an orderly fashion. This alteration of the chloroplast structure by the different light qualities seems to become one of the important factors of photosynthesis; Akoyunoglou and Anni (1984) and our results suggest that blue light is one of the essential factors for chloroplast development.

Starch is synthesized in chloroplast, the quantity being affected by light quality. Compared with red light, blue light accumulated fewer starch grains (Saebo et al., 1995). Zhang et al. (2010) also found that the volume of starch grains was reduced significantly in chloroplast when supplemented blue light on a base of red light. Our result is similar to their reports. The reduction in starch grain volume is mainly the result of the observation that red light inhibits photosynthetic products to be translocated from leaves, and starch was accumulated in leaves (Saebo et al., 1995). This also indicates supplemental blue light on a base of red light can decrease starch content in chloroplasts. However, the excessive accumulation of starch grains is not beneficial to photosynthesis (Bondada and Syvertsen, 2005). This is probably one of the reasons why P_n under R is less than those under B, RB, and RBG in our results.

Mesophyll tissues in cherry tomato leaves exhibited the greatest sensitivity to spectral changes and were apparently most responsive to the presence of blue light. Palisade and spongy tissue cells of leaves under RB, RBG, B, and C developed better than those under R, O, and G, and the best development was under RB and RBG (Fig. 4; Table 3). The thickness of leaves was also increased under spectra containing blue light (Table 2). Schuerger et al. (1997) found similar results in pepper. These phenomena showed a tendency similar to the activity of P_n (Table 3; Fig. 2). In short, the enhancement of the leaf thickness and P_n resulting from blue light seems to be concerned with the well-developed structure of palisade tissue cells in leaves.

Stomatal movement is controlled by various environmental and endogenous factors (Gorton et al., 1993; McDonald, 2003). Light is of major importance with opening in the light and closing in the dark. Kim et al. (2004) indicated that chrysanthemum plantlets under red and blue light, had the smallest number and largest leaf stomata, whereas those under blue and far-red light had the largest number and smallest leaf stomata. In the present study, the number of stomata in the epidermis of leaves under the spectra containing blue light was greater than that under the other light treatments. The distribution, number per unit epidermis area, size (area surrounding with two guard cells), and opening or closing situation of stomata in the leaves greatly influence photosynthesis, transpiration, and the other physiological activities (Sun, 2008). Therefore, these phenomena seem to probably enhance P_n under the respective treatments of RB, RBG, and B.

In conclusion, leaf thickness and length of palisade tissue cells of cherry tomato seedlings were significantly increased by the light in treatments B, RB, and RBG. Chloroplasts

developed well and stomata localized densely under the respective treatments of B, RB, and RBG. The number of grana and lamella structure forming grana stacked densely and orderly was increased as a result of the respective blue light treatments within B, RB, and RBG LEDs. These phenomena seem to cause the enhancement of the P_n of tomato leaves irradiated with B, RB, or RBG light. This result also suggests that blue light is probably necessary light for growth of cherry tomato.

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