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BRIEF COMMUNICATION

Photosynthesis and leaf development of cherry tomato seedlings under different LED-based blue and red photon flux ratios

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Abstract

We investigated the photosynthesis and leaf development of cherry tomato seedlings grown under five different combinations of red and blue light provided by light-emitting diodes (LEDs). Fresh biomass increased significantly under treatments with blue light percentages of 50, 60, and 75%, with 50% blue-light-grown seedlings accumulating significantly more dry mass. The 25% blue-light-grown seedlings were obviously weaker than those from the other LED treatments. An increase in net photosynthetic rate upon blue light exposure (25–60%) was associated with increases in leaf mass per unit leaf area, leaf area, leaf density, stomatal number, chloroplast and mesophyll cell development, and chlorophyll contents. Our results imply that photosynthesis and leaf development in cherry tomato seedlings are associated with both the proportion and quantity of blue light.

Additional key words: chloroplasts; leaf density; mesophyll cell; morphology; stomata.

Cherry tomato is currently one of four the most popular fruits in China, where it is cultivated year round. Winter, late autumn, and early spring in China are characterized by cold temperatures. To prevent stress from such unfavorable growth conditions, cherry tomato seedlings can be cultivated in controllable artificial facilities, but the optimal light environment to produce strong and healthy cherry tomato seedlings in these facilities still needs to be determined.

A combination of red and blue light, the two spectral regions the most essential for plant growth, is increasingly used in plant research and can be used for the commercial cultivation of horticultural crops in controlled and semi-controlled environments (Hogewoning *et al*. 2010, Samuolienė *et al*. 2010, Fan *et al*. 2013a, Miao *et al*. 2016). Studies involving artificial light have suggested that plant responses to relative percentages of red and blue light are species-specific (Hogewoning *et al*. 2010, Liu *et al*. 2011, Cope *et al*. 2014). Even within the same species, however, inconsistent results have been obtained because of different environmental conditions (Liu *et al*. 2011, Nanya *et al*. 2012). Consequently, additional research on the response of individual species to red and blue light percentages is warranted.

Green leaves absorb 85–90% of red and blue light (Terashima *et al*. 2009), but the amount of light sufficient for plant growth and photosynthesis is unknown for cherry tomato grown at red and blue light. Sieve and detour effects have an impact on the absorptance of red and blue light (Terashima *et al*. 2009). The sieve effect is related to non-uniform distribution of chlorophyll (Chl) in the leaf, while the detour effect is connected with the diffusive nature (*i.e*., is a characteristic that light is irregularly reflected in all directions by rough surfaces) of plant tissues (Terashima *et al*. 2009). Light quality and quantity strongly influence photosynthetic pigment content and plant tissues, with leaf anatomical, physiological, and morphological parameters especially differentiated (Hogewoning *et al*. 2010, Gutu *et al*. 2013). Previous studies of leaf development have concentrated on analyses

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Abbreviations: B – blue light; C_i – intercellular CO_2 concentration; Chl – chlorophyll; CP – chloroplast; CW – cell wall; DM – dry mass; FM – fresh mass; G – grana; LA – leaf area; LD – leaf density; LMA – leaf mass per unit leaf area; PT – palisade tissue cells; S – stroma; SG – starch grain; SPT – spongy tissue cells.
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of mesophyll cells, chloroplasts, and stomata under visible monochromatic light (Schuerger *et al*. 1997, Su *et al*. 2014, Wang *et al*. 2015), whereas regulation of leaf microstructure by different proportions of red and blue light has been rarely addressed. Compared with monochromatic light, a combination of red and blue light has a positive effect on chloroplast and leaf mesophyll cell development (Liu *et al*. 2011). Various studies have found that a suitable proportion of red and blue light accelerates photosynthesis and growth of cucumber and lettuce (Hogewoning *et al*. 2010, Xu *et al*. 2015a). Different plant species, or the same species at different growth stages, show diverse responses to the same light wavelength and display complexity and instability of photobiological reactions (Xu *et al*. 2015b). We previously discovered that cherry tomato seedlings are healthier and stronger when grown under a combination of 50% red and 50% blue light than when cultivated under monochromatic light (Liu *et al*. 2011, Fan *et al*. 2013a). Nevertheless, some issues still remain to be resolved, such as whether other proportions of red and blue light can also meet the growth demands of cherry tomato seedlings and how the detour effect caused by leaf differentiation affects their photosynthesis.

In this study, in order to evaluate the response of leaf microstructure and photosynthesis to changes in red–blue light composition and to determine the optimum ratio of red to blue light for culturing cherry tomato seedlings, we investigated photosynthetic rate, chloroplast ultrastructure, leaf anatomical structure, stomatal characteristics, and growth of cherry tomato seedlings under various proportions of red and blue LED composite light. Seeds of cherry tomato (*Solanum lycopersicum* Mill. 'Qianxi') were germinated in culture plates. When roots were 2–3 mm long, the seedlings were transferred to plastic pots containing a mixture of peat and vermiculite (3:1, v/v). With a dysprosium lamp used as a control (white light, C; *LZ400D/H*, 400W; *YaHuaNing Co*., Nanjing, China), the seedlings were exposed to one of five different combinations of red and blue LEDs: all blue light (100B) or blue:red PPFD ratios of 3:1 (75B), 3:2 (60B), 1:1 (50B) or 1:3 (25B). Peak wavelengths of red and blue LEDs were, respectively, 450 and 660 nm, with a width at half height of 15 nm. All light treatments were set up at the same PPFD level of 300 ± 10 μmol(photon) m^{-2} s^{-1}. The reasons for the choice of this growth irradiance were discussed in our previous work (Fan *et al*. 2013a). Compared to higher PPFD, this irradiance has a greater photosynthetic rate per PPFD of cherry tomato seedlings at all irradiation spectra studied (Liu *et al*. 2010). The plants were grown under a 12-h light/12-h dark period, day and night temperatures of 28 ± 2ºC/18 ± 2ºC, a relative humidity of 60–80%, and a CO_2 concentration identical to concentrations in the outdoor atmosphere. Each treatment consisted of 30 plants, all having roughly the same morphology.

After 30 d of light irradiation, the method of Chang *et al*. (2010) was used to obtain the area of the third fully expanded leaf (LA) counting from the top of the plant. After root washing, to determine the dry mass (DM) of each plant, plants were dried at 80ºC until a constant mass. Fresh mass (FM) and DM were measured using an electronic balance (*BSA124S*, *Sartorius*, Beijing, China). Leaf mass per unit area (LMA) and leaf density were calculated as follows: LMA = leaf DM/LA; and leaf density (LD) = 1000 × leaf DM/(LA × leaf thickness). Statistically, LAs of 100B plants were significantly larger than LAs of 75B, 50B, and C treatments. The trend exhibited by LMA with an increasing proportion of blue light resembled a sine curve: 50B and 60B leaves had larger LMAs and 25B leaves had smaller ones. LDs of LED-treated plants, especially 60B and 50B, significantly increased compared with the C treatment. FMs of plants under 75B, 60B, and 50B were not significantly different from one another but were significantly higher than those of other treatments. The DM of 50B seedlings was significantly greater than that of 75B and 60B plants. Plants from 25B and especially C treatments had the lowest FM and DM values (Table 1).

Chl were characterized using the method of Fan *et al*. (2013b). The net photosynthetic rate (P_N) of fully expanded third leaves were measured using a photosynthesis meter (*LI-6400*; *LI-COR*, Lincoln, NE, USA). Measurements were made under a PPFD of 800 μmol m^{-2} s^{-1}, with a leaf temperature, CO_2 concentration, and relative humidity of 23 ± 1°C, 380 ± 5 μL L^{-1}, and 60–70%, respectively. When the percentage of blue light ranged from 25 to 75%, Chl *a*, Chl *b*, and Chl (*a*+*b*) contents remained constant. Chl contents of 100B-grown leaves were significantly lower than those of 60B-grown ones. An increase in the fraction of blue light from 25 to 60% resulted in an increase in the net photosynthetic rate (P_N), which then decreased in 75B and increased again in 100B. The lowest recorded P_N among treated plants was in leaves from the 25B treatment, while the P_N of C-grown leaves was even smaller. No significant difference was observed in P_N between 100B and 60B leaves (Table 1).

Leaf samples were collected for 30 d approximately 3 h after the start of daily irradiation. Chloroplasts were prepared, observed, and photographed as described by Liu *et al*. (2011). Anatomical analysis of leaf mesophyll cells of cherry tomato seedlings was carried out according to the method of Yao *et al*. (2007), with their structures examined under an optical microscope (*DP71*, *Olympus*, Tokyo, Japan). Leaf palisade (PT) and spongy tissue (SPT) lengths were measured with a light microscope connected to an imaging analysis system. The compactness of SPT and PT are based on ratios of areas on leaf profiles to calculate. The compactness of SPT = (SPT area – intercellular air space area)/SPT area; the compactness of PT = (PT area – intercellular air space area)/PT area. Stomata of the leaf upper epidermis were sampled and analyzed according to Duan *et al*. (2008). The number of leaf epidermis stomata per field of vision was converted to the number per mm^2. The data demonstrated that, as the proportion of blue light was increased, leaf thickness decreased except for 50B,

Table 1. Parameters measured or calculated on leaves grown under different combinations of red and blue LED light. Within each column, values labeled by different *lowercase letters* are significantly different ($P \leq 0.05$). Chl – chlorophyll; DM – dry mass; FM – fresh mass; LA – leaf area; LD – leaf density; LMA – leaf mass per unit leaf area; P_N – net photosynthetic rate; PT – palisade tissue cells; SPT – spongy tissue cells. All data were subjected to one-way analysis of variance using *SPSS 18.0* for *Windows* (*SPSS*, Chicago, IL, USA). Analyzed values corresponded to the means of all measurements. Comparisons of means were performed with *Duncan*'s multiple range test. A difference was considered significant at $P \leq 0.05$.

Parameter	Light treatment					
	100B	75B	60B	50B	25B	C
LA [cm^2]	8.02^{a}	5.91^{bc}	7.04^{ab}	5.13^{c}	5.08^{c}	6.78^{ab}
FM [g per plant]	5.681^{b}	6.642^{a}	6.501^{a}	6.861^{a}	4.798^{c}	4.150^{d}
DM [g per plant]	0.584^{c}	0.653^{b}	0.647^{b}	0.755^{a}	0.491^{d}	0.453^{d}
LMA	170.5^{bc}	152.8^{cd}	180.0^{ab}	193.2^{a}	158.9^{c}	116.1^{d}
LD	0.291^{b}	0.234^{c}	0.346^{a}	0.374^{a}	0.253^{c}	0.135^{d}
Chl *a* [mg g^{-1}(FM)]	2.001^{c}	2.318^{ab}	2.392^{a}	2.300^{ab}	2.196^{abc}	2.068^{bc}
Chl *b* [mg g^{-1}(FM)]	0.933^{b}	1.207^{ab}	1.261^{a}	1.171^{ab}	1.084^{ab}	1.014^{ab}
Chl (*a*+*b*) [mg g^{-1}(FM)]	2.934^{c}	3.525^{ab}	3.654^{a}	3.472^{ab}	3.280^{abc}	3.082^{bc}
P_N [μmol m^{-2} s^{-1}]	20.2^{ab}	16.71^{cd}	21.73^{a}	18.33^{bc}	15.26^{de}	14.55^{e}
Leaf thickness [μm]	44.73^{cd}	47.50^{bc}	49.85^{ab}	42.92^{d}	52.15^{a}	38.47^{e}
The length of PT [μm]	23.10^{a}	22.96^{a}	23.04^{a}	16.25^{c}	23.16^{a}	18.52^{b}
The length of SPT [μm]	17.20^{bc}	18.77^{b}	21.45^{a}	21.70^{a}	21.72^{a}	14.85^{c}
The compactness of PT [%]	82.86^{ab}	82.04^{ab}	88.04^{a}	87.20^{a}	85.26^{a}	73.73^{b}
The compactness of SPT [%]	70.09^{c}	82.50^{b}	83.83^{b}	91.79^{a}	74.68^{c}	67.19^{cd}
The stomata number [mm^{-2}]	685.6^{b}	644.1^{b}	685.6^{b}	914.1^{a}	415.5^{c}	477.8^{c}

where leaves were thinner (exceeding only control leaves) and PT was the shortest. No significant difference was observed in the length of PT among the other red–blue light treatments. No difference was found in the length of SPT in 25–60% B-grown leaves. Increasing the fraction of blue light from 25 to 100% decreased the length of SPT. While the quantity of blue light had no significant effect on the compactness of PT, an increase in the fraction of blue light from 50 to 100% decreased the compactness of SPT. The compactness of SPT was not significantly different between 100B, 25B, and C treatments. The number of stomata in 50B leaves was significantly higher than in other treatments, with the number in 75B, 60B, and 100B leaves significantly higher than that in 25B and C. The smallest number of stomata was recorded in 25B (Table 1).

Compared with control seedlings, starch granules in chloroplasts of 50B seedlings were larger and more numerous, and the increased number of starch granules altered the shape of the chloroplasts. Plants from the 75B treatment had also many large starch granules, whereas 60B, 100B, and 25B chloroplasts had only a few small ones. Grana thylakoids and grana lamellae of all treated leaves were clear except in the 50B treatment, where grana lamellae could not be distinguished because they were obscured by the abundance of large starch granules. In leaves from the 60B treatment, the lamellar was compact structure and was roughly of the same thickness (Fig. 1).

In the current study, the control plants with lower P_N and restricted growth seemed to be a result of the relatively small amount of red and blue light from a light source. The increase in P_N was observed with the LED treatments, except in the case of 100B, the increase in P_N with increasing percentages of blue light (25–75%) was associated with the increase in the Chl content (Table 1). Similar results have been reported for cucumber (Hogewoning *et al*. 2010, Hernández and Kubota 2016). The high Chl content of 60B leaves increased light energy absorption and thus energy for photosynthesis, thereby leading to a higher P_N. In contrast, the Chl content of 25B-grown leaves was very low, which reduced the amount of captured light energy and affected photosynthesis. Increasing the fraction of blue light from 25 to 60% significantly increased P_N (Table 1), similar results were found for cucumber (Hogewoning *et al*. 2010, Hernández and Kubota 2016) and spinach (Matsuda *et al*. 2007). Unlike the results of Hernández and Kubota (2016), however, 75B-grown leaves had P_N lower than that of 60B and 100B leaves (Table 1). Plant response to irradiance differed between high and low light levels. The intensity of blue light used to irradiate cucumber in the study of Hernández and Kubota (2016) was only 75 μmol(photon) m^{-2} s^{-1}, while cherry tomato seedlings in our study were irradiated with blue light of 225 μmol(photon) m^{-2} s^{-1}. In spinach, an increase in blue light intensity from 100 to 150 μmol(photon) m^{-2} s^{-1} was associated with a slight decrease in Chl contents (Matsuda *et al*. 2007). In the present study, similar results were obtained when blue light intensity increased from 180 to 225 μmol(photon) m^{-2} s^{-1}. These results indicate that the observed effects of combined red and blue light on plant growth and development were a response to the quantity as well as the proportion of blue light.

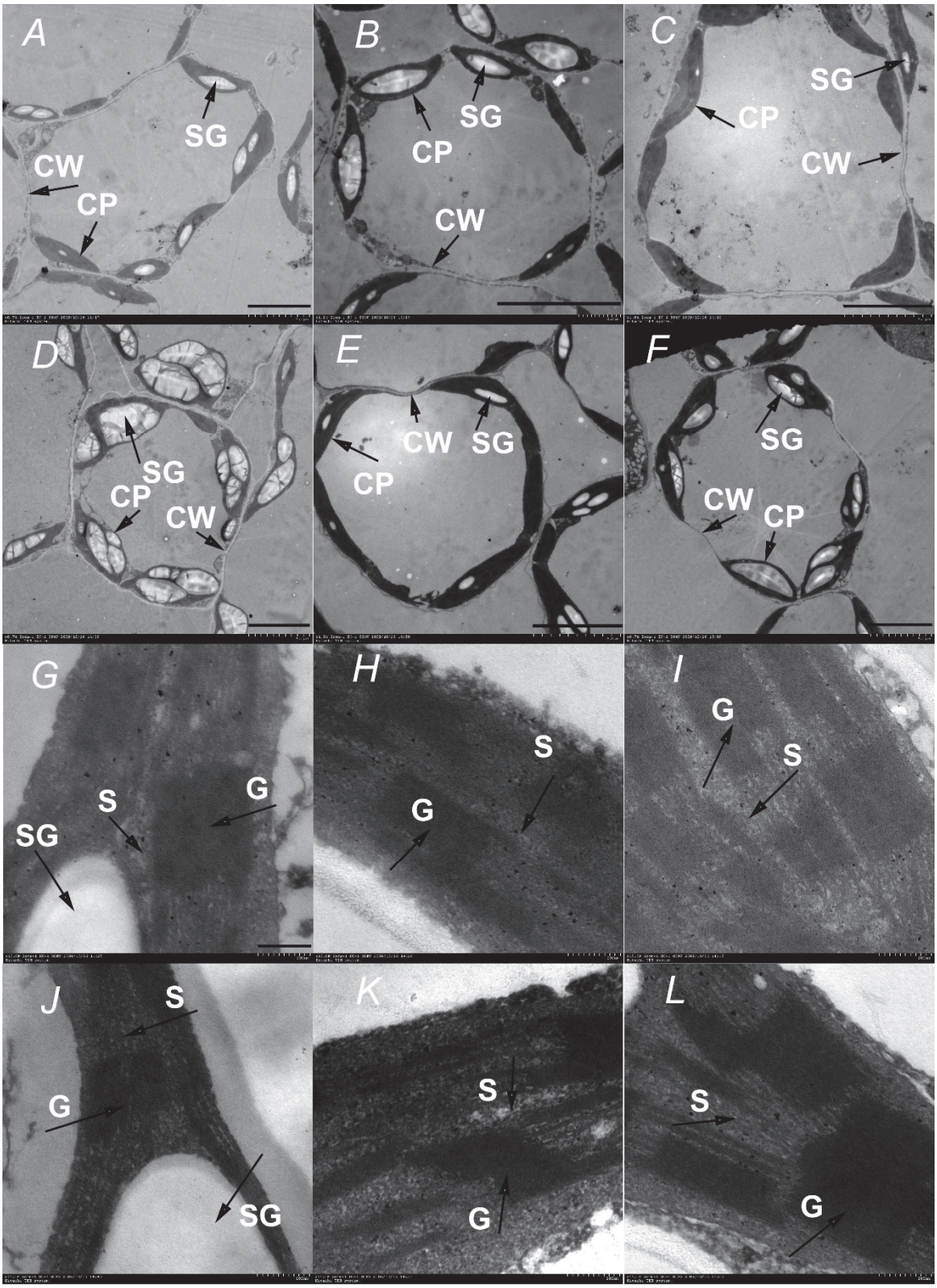

Fig. 1. Effects of different combinations of red and blue LED light on chloroplast ultrastructure of cherry tomato leaves. CP – chloroplast; CW – cell wall; G – grana; S – stroma; SG – starch grain. Images *A* to *F* show the chloroplast ultrastructure of leaves from 100B, 75B, 60B, 50B, 25B, and C treatments, respectively, with *G* to *L* representing corresponding higher-magnified images. Scale bars = 5 μm (*A–F*) and 200 nm (*G–L*).

Despite the above findings, the low Chl content did not inhibit the P_N of 100B-grown leaves (Table 1). The same result has been observed in cucumber (Su *et al*. 2014). The low Chl content and high P_N of 100B was not only associated with Rubisco (Su *et al*. 2014), but was also related to the detour effect caused by leaf differentiation. The thicker PT of 100B leaves partly contributed to their higher P_N (Table 1). Similar results have also been reported for cucumber (Hernández and Kubota 2016). In terms of photosynthesis, thick palisade cells represent an efficient structure (Gonçalves *et al*. 2008). Furthermore, we hypothesize that high LD of 100B leaves (it was only lower than that of 60B- and 50B-grown leaves; Table 1) facilitates the diffusive nature of a leaf and an increase in the light path length (detour effect) and hence the opportunity for light to encounter chloroplasts, thereby leading to an increase in absorptance of 100B leaves (Vogelmann 2003). Our findings suggest that high-LD leaves might increase light absorption and promote photosynthesis.

In this study, compared to other LED treatments, 50B-grown leaves had the thinnest leaves, the shortest PT, and the largest and most abundant starch granules (Table 1, Fig. 1). These characteristics seem to inhibit plant photosynthesis (Gonçalves *et al*. 2008, Matos *et al*. 2009), as smaller mesophyll cells can decrease internal leaf surface area and the weaker aerenchyma can reduce photosynthetic efficiency. Although having the greatest DM, however, 50B-grown leaves had P_N values that were higher than those of all other treatments except for 60B and 100B (Table 1), but they had also the highest stomata number, and PT and SPT compactness values. An increase in stomata number is associated with increased photosynthesis (Lawson *et al*. 2011, Fan *et al*. 2013a). The highly compact state of PT and SPT in 50B-grown leaves would imply more palisade and spongy cells and a smaller number of intercellular air spaces per unit area. We propose that in 50B-grown leaves with their high refractive index, the diffusive nature of leaf tissues could be more pronounced and hence could increase the light path length and partially compensate for reduced photosynthesis caused by thin leaves and short PT (Vogelmann 2003, Terashima *et al*. 2009). In 25B- and C-treated plants, photosynthesis was also reduced as a result of smaller leaves, lower Chl contents, LMA and LD, and sparse PT and SPT (Table 1). The lesser number of stomata in 25B- and C-grown leaves lowered the P_N by increasing diffusive resistance to CO_2 uptake, a process that may reduce the burden on photosynthetic organs (Lawson *et al*. 2011). According to one study, as the number and volume of starch granules increased, the entire chloroplast was filled, which severely limited the distribution of stroma and grana lamellae and caused a loss of structural integrity, eventually leading to its reduced photosynthetic function (Wang *et al*. 2015). Persistent accumulation of starch in the chloroplast is a reflection of depressed translocation and severely impairs chloroplast structure and function (Paul and Foyer 2003). Although 50B-grown leaves indeed had a lower P_N than did lower-starch 60B and 100B leaves, the DM was higher. Starch granules in chloroplasts of 50B-grown leaves may be temporary rather than persistent (Xu *et al*. 2015b), as our results suggest robust photosynthesis in 50B-grown leaves, with more photosynthates produced at the time of sample collection.

In conclusion, the amount of blue light had a marked effect on LA, LMA, and LD and the development of mesophyll cells, chloroplasts, and stomata of cherry tomato seedlings, but only a slight impact on the Chl content. Blue light proportions of 50–75%, and especially 50%, accelerated fresh biomass production. Treatment with lower blue light levels (25%) inhibited seedling growth. In cherry tomato seedlings, photosynthesis and leaf development were influenced by the quantity as well as the proportion of blue light.

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