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Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light

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ABSTRACT

We used red light-emitting diodes (LEDs, R) and blue light-emitting diodes (LEDs, B) to obtain the different light intensities of uniform spectra and investigated the effects of different light intensities on growth and leaf development of young tomato plants. The results showed that fresh weight, dry weight, stem diameter and health index were superior in plants grown under 300, 450 and 550 μmol m^{-2} s^{-1}. The energy efficiency was highest under 300 μmol m^{-2} s^{-1}. When photosynthetic photon flux density (PPFD) increased from 50 to 550 μmol m^{-2} s^{-1}, a decrease in the specific leaf area (SLA) was observed. Under 300 and 450 μmol m^{-2} s^{-1}, the thickness of leaves, palisade parenchyma and spongy parenchyma were the bigger, and the stomatal frequency and stomatal area per unit leaf area were also higher. The highest net photosynthesis rate (Pn) was observed under 300 μmol m^{-2} s^{-1}. Our results implied that, compared to other light treatments, 300 μmol m^{-2} s^{-1} was more suitable for the culture of young tomato plants and there was no substantial gain from a PPFD above 300 μmol m^{-2} s^{-1}.

1. Introduction

As a primary source of energy, light is one of the most important environmental factors for plant growth (Naoya et al., 2008). The intensity and quality of light are essential for the growth, morphogenesis and other physiological responses of plants (Rajapakse et al., 1992; Fukuda et al., 2008; Li and Kubota, 2009).

Changes in the spectrum of light strongly influenced the parameters of the anatomy, physiology and morphology of leaves (Hogewoning et al., 2010; Macedo et al., 2011). It has been shown that the blue spectrum increased the thickness of the epidermis and palisade mesophyll cells, whereas the red spectrum decreased the thickness of the abaxial-face and spongy tissues (Saebo et al., 1995; Macedo et al., 2011).

The light intensity is also an important factor for plant growth. Low-light grown plants have frequently been shown to be more susceptible to photoinhibition than those plants grown under high light intensity (Long et al., 1994). Usually, the increases in net photosynthesis rate (Pn) correlates with increases in light intensity. However, high light intensity resulted in decreases of net photosynthesis rate (Bowes et al., 1971; Khatib and Paulsen, 1989). In order to adjust the various light environments, plants have evolved many mechanisms, including morphological and physiological changes at the levels of the leaf (Zhang et al., 2003). Low light levels may lead to increase in specific leaf area (SLA) and plant height. These adaptations maximize the capture of the available light, meeting the demand for photosynthesis (Steinger et al., 2003). Whereas, high irradiances are related to many acclimating morpho-physiological characteristics, such as reduction in specific leaf area (SLA) in order to protect the plant from high irradiance; increase in leaf thickness, due to the quantity of layers or growth of palisade tissue; deep development of spongy layer. These measures prevent or mitigate light damage caused by excessive light energy, ensuring the proceeding of photosynthesis (Givnish et al., 2004; Matos et al., 2009; Morais et al., 2004; Sims and Pearcy, 1994; Wentworth et al., 2006).

The percentage absorption of blue or red light by plant leaves is about 90% (Terashima et al., 2009). Thus, plant development and physiology are strongly influenced by blue or red light (McNellis and Deng, 1995). The combination of red and blue light is used nowadays more and more in research but also commercial horticulture because they are the most photosynthetic effective wavebands at leaf level in short terms (McCree, 1972) and long terms (Hogewoning et al., 2010). The absence of one of the two light wavebands (red or blue) creates photosynthetic inefficiencies (Hogewoning et al., 2010).

The combination of red and blue light was an effective lighting source to plant development (Wheeler et al., 1991), and promote

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the plant health (Nhut et al., 2003). The combination of red and blue in 1:1 ratio might promote fresh weight and dry weight in many plant species such as Lilium, Chrysanthemum and tomato (Lian et al., 2002; Kim et al., 2004; Liu et al., 2011). When cultured under B:R = 1:1 LED light, the plants had higher specific leaf area (Heo and Lee, 2006; Li et al., 2010), which might enhance light absorption. The B:R = 1:1 also caused the enhancement of the Pn of plant leaves (Kim et al., 2004; Lee et al., 2007; Liu et al., 2011).

Previous researches have been mainly focused on the effects of different light intensities on the growth and development of plants in the natural sunlight. However, very little is known about the effects of different light intensities on the growth and development of plants under the combination of red and blue light. What effects will different artificial light intensities, especially those of the combined red and blue light, have on the growth and development of plants? And which artificial light intensity will be suitable for the culture of plants? For these reasons, it is necessary to investigate the suitable light intensities of red and blue LEDs combined for the industrialized production and to evaluate different response caused by the low and high light intensity in the artificial conditions.

Tomato (*Lycopersicon esculentum* Mill *qianxi*) is a crop widely distributed in the world and is cultivated in China throughout the year. The young tomato plants are mainly produced under controlled conditions on a large scale to meet the increasing production demand. In a controlled environment, supplemental lighting is often used from fall to spring to enhance seedling growth and to obtain year-round high production and good quality (Kozai, 2007). Therefore, because the light is the most important factor affecting the growth of young tomato plants in a controlled environment, further study is required.

It was reported that the combination of red and blue LEDs (R:B = 1:1) was more effective for the growth of cherry tomato plants. The light sources of B:R = 1:1 caused the enhancement of the Pn of tomato leaves, and palisade tissue cells and chloroplasts in leaves were especially well-developed (Liu et al., 2011). In this study, we used red and blue LEDs (R:B = 1:1 Liu et al., 2011) to obtain the different light intensities with uniform spectra, with the objective of investigating the effects of light intensities on leaf development and to identify the suitable light intensities for the culture of young tomato plants.

2. Materials and methods

2.1. LEDs devices with different light intensities

All of the combined LEDs had the uniform spectra of red and blue, and were designed by College of Agriculture, Nanjing Agricultural University, China. The spectral distribution of the blue (peak at 460 nm) and red (peak at 658 nm) light were measured using a spectroradiometer (OPT-2000, ABDPE CO., Beijing, China). Light treatments for the young tomato plants were 50, 150, 200, 300, 450 and 550 $\mu mol\,m^{-2}\,s^{-1}$. In each treatment, photosynthetic photon flux density (PPFD) of the red and blue LEDs were equal (Hogewoning et al., 2010; Liu et al., 2011) and the LED array was supplied with 50% blue light intensity and 50% red light intensity (B:R = 1:1). PPFD was measured using a quantum sensor (LI-250, LI-COR, USA) and was separately controlled by adjusting both the electric currents and numbers of light bulbs for the LEDs. The parameters of the light in each treatment are shown in Table 1.

All of the treatments were placed in a culture room and were arranged in as separate plots with different light intensities. There was ventilation in the controlled environment, so the CO_2 level was the same as the CO_2 level of atmosphere outside. The relative humidity (RH) was maintained at 70 ± 10%, with a 12 h photoperiod and a temperature of 28 °C during daytime and 18 °C at night.

Table 1
Major light parameters of treatments.

Treatment	Light intensity ($\mu mol\,m^{-2}\,s^{-1}$)	Peak wavelength λ_p (nm)	Halfwave width $\Delta\lambda$ (nm)
R + B (1:1)	50	658 + 460	±12 and ±11
R + B (1:1)	150	658 + 460	±12 and ±11
R + B (1:1)	200	658 + 460	±12 and ±11
R + B (1:1)	300	658 + 460	±12 and ±11
R + B (1:1)	450	658 + 460	±12 and ±11
R + B (1:1)	550	658 + 460	±12 and ±11

2.2. Plant materials

Seeds of cherry tomato (*Solanum lycopersicum Mill qianxi.*) provided by Taiwan Farmers Co., were planted in plastic pots containing a mixture of peat and vermiculite (3:1, v/v). When the second leaves were fully expanded, 120 young tomato plants were randomized into 6 groups and were placed under 6 light treatments for 30 days. All measurements were carried out using the third fully expanded leaf counted from the top of the plant.

2.3. Biomass and growth parameter analysis

A total of 30 young plants for each treatment were randomly selected and destructively sampled for biomass analysis after 30 days of growth. To determine the dry weight, the young plants were dried at 85 °C until a constant mass was reached. The weight of the young plants was then measured using an electronic balance. The plant height was measured from the main stem base to the top of the young plants using a ruler, and the stem diameter was measured at the internode above cotyledons using vernier calipers. The growth and morphology experiment was repeated 6 times with 5 plants in each treatment.

The specific leaf area of each young plant was measured using the equation:

$$\text{Specific leaf area (SLA)} = \frac{\text{Leaf area}}{\text{Leaf dry weight}}$$

The health index was determined using the following equation:

$$\text{Health index} = \frac{\text{Stem diameter}}{\text{Stem height}} \times \text{Dry weight}$$

The Energy efficiency was determined using the following equation:

$$\text{Energy efficiency} = \frac{\text{Dry weight}}{\text{Power consumed by LEDs}}$$

2.4. Morphological and physiological analyses

2.4.1. Anatomical features of leaf

The anatomical analysis of the mesophyll cells in the leaves of the young plants was performed using the method of Clark (1981). The anatomical structure of the mesophyll cells of the leaves was examined under a light microscope (DP71, OLYMPUS Inc., Japan). We analyzed 10 images per leaf, one leaf per plant and 5 plants per treatment. The experiment was repeated 6 times. Leaf thickness, length of palisade cells and parenchyma cells were calculated from 30 epidermis measurements.

2.4.2. Stomatal traits

Portions of the epidermis were removed from the middle of the leaf with a razor blade, stained with a mixture of 1:1 (v/v) 50% aqueous ethanol and safranin (1% in water), and mounted in 1:1 (v/v) glycerol:water (Jensen, 1962). Slides were analyzed using an Olympus DP71 microscope (Olympus Inc., Japan), and the single

Table 2
Effects of different light intensities on morphology of young tomato plants.

Light treatment ($\mu mol\ m^{-2}\ s^{-1}$)	Dry weight (g)	Fresh weight (g)	Plant height (cm)	Stem diameter (mm)	Specific leaf area (cm^2/g)	Health index	Energy efficiency (g/kw)
50	0.20e	2.64c	22.43a	3.23c	114.69a	0.03c	5.56d
150	0.39d	4.11b	15.77b	3.51bc	71.99b	0.09bc	7.22b
200	0.48c	4.60ab	16.06b	3.67ab	61.84bc	0.11b	6.60c
300	0.59b	5.18a	11.78c	3.75ab	52.13cd	0.19a	8.19a
450	0.57b	4.65ab	12.16c	3.95a	44.57d	0.19a	6.33c
550	0.66a	5.41a	12.79c	3.98a	44.36d	0.21a	5.24d

Different letters in columns indicate statistically significant differences ($P < 0.05$).

stomatal pore area and stomatal pore area per unit were measured using Motic Images Plus 2.0 (Wang et al., 2009). We analyzed 10 images per leaf, one leaf per plant and 5 plants per treatment. The experiment was carried out 6 times.

2.4.3. Net photosynthesis rate (Pn)

Net photosynthesis rate (Pn) was made out using a photosynthesis instrument (LI-6400, LI-COR, USA). PPFD was set to measure at 800 $\mu mol\ m^{-2}\ s^{-1}$, and the experimental conditions such as leaf temperature, CO_2 concentration and relative humidity (RH) were $23 \pm 1\ ^{\circ}C$, $380 \pm 5\ \mu L\ L^{-1}$ and 60–70%, respectively. The Pn experiment was repeated 3 times with 3 plants in each treatment.

2.5. Statistical analyses

Statistical analyses were conducted using Statistical Product and Service Solutions for Windows, version 16.0 (SPSS Inc., Japan). The data were analyzed using analysis of variance (ANOVA), and the differences between the means were tested using Duncan's multiple range test ($P < 0.05$).

3. Results

3.1. Morphology

The morphology of the cherry young tomato plants was found to be significantly different under different light intensities (Table 2). 50 $\mu mol\ m^{-2}\ s^{-1}$ induced the lowest biomass, stem diameter and health index in plants, and 550 $\mu mol\ m^{-2}\ s^{-1}$ induced the highest biomass, stem diameter and health index. PPFD of 50, 150 and 200 $\mu mol\ m^{-2}\ s^{-1}$ induced, in that order, significantly longer stem and lower fresh weight, dry weight, stem diameter and health index than the values of other young plants. When PPFD increased from 50 to 550 $\mu mol\ m^{-2}\ s^{-1}$, a decrease in the SLA was observed. The PPFD of 300 $\mu mol\ m^{-2}\ s^{-1}$ or greater increased the biomass and heath index of the young tomato plants. Under 300 $\mu mol\ m^{-2}\ s^{-1}$, the energy efficiency was the highest and there was no substantial gain from a PPFD above 300 $\mu mol\ m^{-2}\ s^{-1}$.

3.2. Palisade parenchyma and spongy parenchyma

Light, especially the light intensity, seemed to positively affect the leaf structure of the palisade parenchyma and spongy parenchyma (Table 3, Fig. 1). The leaves under the 50 $\mu mol\ m^{-2}\ s^{-1}$ presented imperfect development of the palisade parenchyma, and a more compact and clear structure of the palisade cells was observed under other treatments. The leaf thickness, length of palisade cells and parenchyma cells were bigger in the seedlings grown under 300 and 450 $\mu mol\ m^{-2}\ s^{-1}$. There was no significant different in leaf structure between 300 and 450 $\mu mol\ m^{-2}\ s^{-1}$.When PPFD increased from 50 to 300 $\mu mol\ m^{-2}\ s^{-1}$, the thickness of the leaf blade, palisade cells and parenchyma cells increased. However, the seedlings grown under the high PPFD of 550 $\mu mol\ m^{-2}\ s^{-1}$ exhibited shorter mesophyll cells (Table 3, Fig. 1F).

Table 3
Effects of different light intensities on structure in young tomato plants leaves.

Light treatment ($\mu mol\ m^{-2}\ s^{-1}$)	Length of palisade cells (μm)	Length of parenchyma cells (μm)	Thickness of leaves (μm)
50	24.17c	25.89d	58.69d
150	29.11c	35.08c	75.88d
200	32.87b	36.76c	81.88c
300	35.64a	58.56a	113.72a
450	35.10a	55.8a	109.50a
550	34.10b	44.76b	93.78b

Different letters in columns indicate statistically significant differences ($P < 0.05$).

3.3. Stomatal traits

The different light intensity resulted in different distributions of the stomata traits (Table 4, Fig. 2). The highest stomatal frequency and stomatal area per unit leaf area were observed on the abaxial face under the 300 $\mu mol\ m^{-2}\ s^{-1}$ (Table 4, Fig. 2D), whereas the lowest stomatal frequency and stomatal area per unit leaf area were observed under 50 $\mu mol\ m^{-2}\ s^{-1}$ (Table 4, Fig. 2A). When PPFD decreased from 300 to 50 $\mu mol\ m^{-2}\ s^{-1}$ or increased from 300 to 550 $\mu mol\ m^{-2}\ s^{-1}$, a gradual decrease in the stomatal frequency and stomatal area per unit leaf area was observed. There was no significant different in stomatal area per unit leaf area among 300, 450 and 550 $\mu mol\ m^{-2}\ s^{-1}$. Light intensity did not cause any significant effect on single stomatal pore area.

3.4. Net photosynthesis rate (Pn)

The Pn of leaves was highest under 300 $\mu mol\ m^{-2}\ s^{-1}$ and lowest under 50 $\mu mol\ m^{-2}\ s^{-1}$. When PPFD increased from 50 to 300 $\mu mol\ m^{-2}\ s^{-1}$, an increase of the Pn was observed. However, PPFD exceed than 300 $\mu mol\ m^{-2}\ s^{-1}$, the Pn significantly decreased (Fig. 3).

4. Discussion

The structure of plants is regulated, in part, by light signals from the environment (Hoenecke et al., 1992; Franklin et al., 2005; Kim et al., 2007). Light is the energy source for photosynthetic organisms, and light intensity plays an important role in

Table 4
Effects of different light intensities on stomata traits in young tomato plants leaves.

Light treatment ($\mu mol\ m^{-2}\ s^{-1}$)	Single stomatal pore area (μm^2)	Stomatal frequency (ind/mm^2)	Stomatal pore area per unit leaf area (mm^2/cm^2)
50	37.13a	1108.53c	4.11c
150	38.98a	1189.04c	4.67c
200	38.31a	1616.35b	6.17b
300	38.26a	1882.64a	7.32a
450	38.86a	1678.28b	6.40ab
550	39.65a	1603.96b	6.37ab

Different letters in columns indicate statistically significant differences ($P < 0.05$).

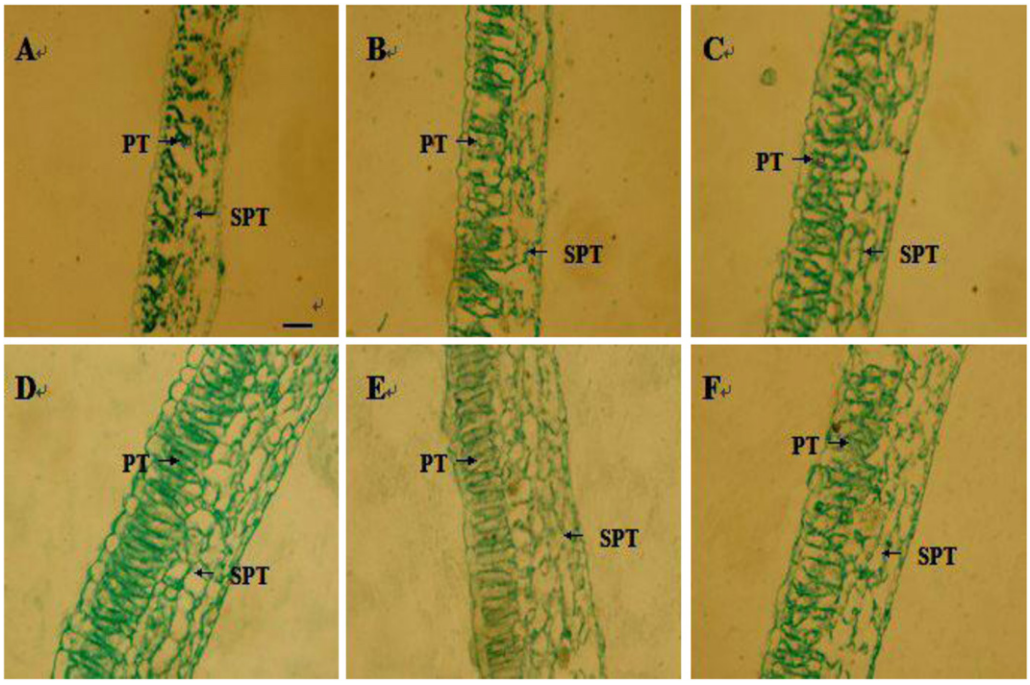

Fig. 1. Effects of different light intensities on anatomical structure in young tomato plants leaves. (A: 50 μmol m^{-2} s^{-1}, B: 150 μmol m^{-2} s^{-1}, C: 200 μmol m^{-2} s^{-1}, D: 300 μmol m^{-2} s^{-1}, E: 450 μmol m^{-2} s^{-1}, F: 550 μmol m^{-2} s^{-1}). PT, palisade parenchyma; SPT, spongy parenchyma. Scale bar is 25 μm.

plant growth. Low light conditions inhibit plant growth and productivity by affecting gas exchange (Zavala and Ravetta, 2001), whereas excess light intensity has detrimental effects on the photosynthetic apparatus (Lichtenthaler et al., 2007). As a result, plants have developed sophisticated mechanisms to adapt their structure and physiology to the prevailing light environment. In our study, the low PPDF of 50, 150, and 200 μmol m^{-2} s^{-1} induced lower health index for young tomato plants, indicating that low PPFD were not suitable for their growth (Table 2). Along with the increase of the light intensity, SLA always gradually

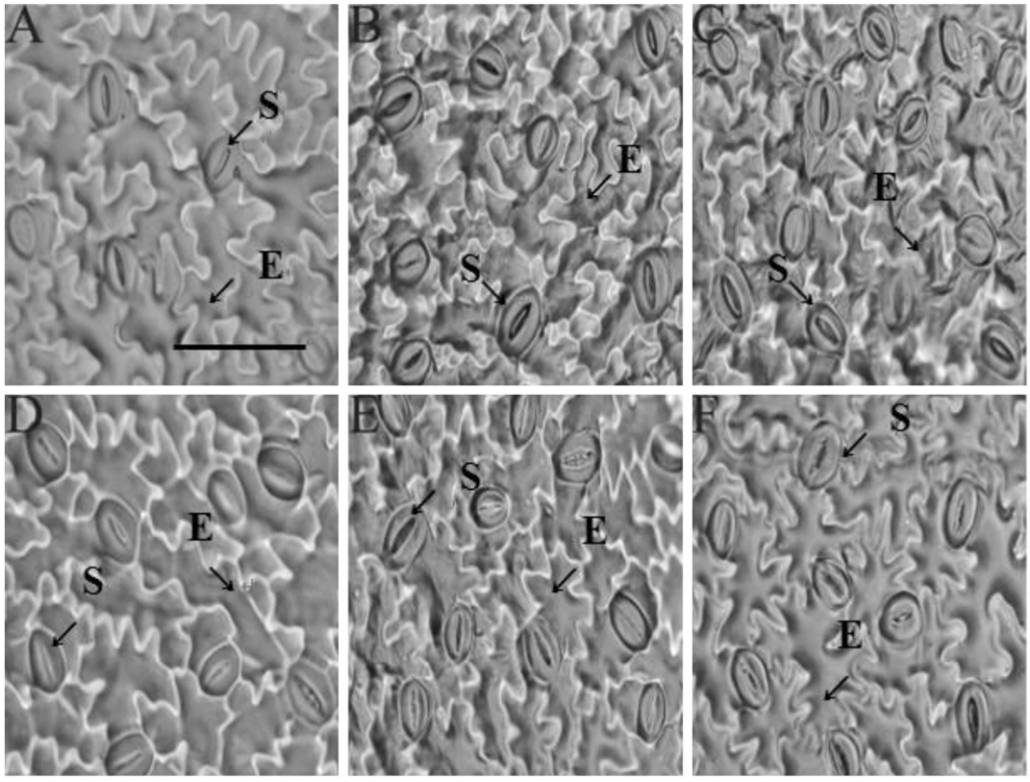

Fig. 2. Effects of different light intensities on stomata traits in young tomato plants leaves. (A: 50 μmol m^{-2} s^{-1}, B: 150 μmol m^{-2} s^{-1}, C: 200 μmol m^{-2} s^{-1}, D: 300 μmol m^{-2} s^{-1}, E: 450 μmol m^{-2} s^{-1}, F: 550 μmol m^{-2} s^{-1}). S, stomata; E, epidermis. Scale bar is 25 μm.

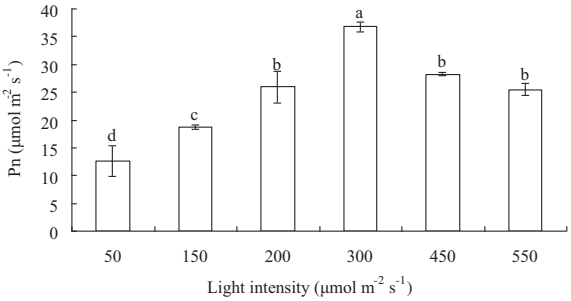

Fig. 3. Effects of different light intensities on net photosynthesis rate (Pn) of young tomato plants. Letters (a, b, c, d) indicate statistically significant differences between the means ($P < 0.05$) using LSD with SPSS.

decreased, and the decrease in SLA may reduce the light energy absorption.

If the excessive light energy that has been absorbed by photosynthetic apparatus cannot be dissipated rapidly, it may reduce the photosynthetic efficiency and results in photoinhibition and even damage to the photosynthetic reaction center. For instance, photosystem I can be readily photoinhibited by high light stress, and high light also inhibit the repair of photosystem II (Takahashi and Murata, 2008). In this study, although the high PPDF of 450 and 550 μmol m^{-2} s^{-1} promoted the higher fresh weight, dry weight and health index of the young plants (Table 2), this was marginally so, and the analysis of the leaf structure, stomata traits and Pn (Tables 3 and 4, Fig. 3) showed that the high light probably caused damage to the photosynthetic organelles.

Photosynthetic light acclimation involves a variety of responses, including changes in leaf anatomy (Weston et al., 2000). The palisade parenchyma and spongy parenchyma in mesophyll cells are important photosynthetic tissues. Palisade tissue enables a better light penetration to the chloroplasts, while spongy tissue enhances the light capture by scattering light (Evans, 1989). Our results showed that, under the PPFD of 300 and 450 μmol m^{-2} s^{-1}, the leaf thickness and length of palisade cells were longer (Table 3, Fig. 1D–F). The thickness of palisade cells presented an efficient structure in terms of photosynthesis (Goncalves et al., 2008). Terashima and Saeki (1983) found that increases in PPFD correlated with decreases in leaf thickness and this correlation is due to the short palisade parenchyma and spongy parenchyma. We also found that the high PPFD of 550 μmol m^{-2} s^{-1} resulted in decreases of the leaf thickness (Table 3, Fig. 1F) and smaller SLA (Table 2), which were able to avoid or reduce light inhibition and adapt themself to changes of light and protected the photosynthetic structures (Sims and Pearcy, 1994; Wentworth et al., 2006).

The stomata are important channels for the exchange of water and air with the external environment, and light intensity influences the stomata conductance by enhancing the motive force of protons (Hattori et al., 2007). Moreover, development of stomata also appears to be related with light intensity (Lee et al., 2007). Our results agreed with the studies in which a quantitative analysis demonstrated that the stomatal frequency increased as light intensity increased (Gorton et al., 1993; Thomas et al., 2003). We found that a progressive increase in stomatal frequency and stomatal pore area per unit leaf area was recorded with increasing light intensity, while light intensity did not cause any significant effect on the single stomatal pore area (Table 4). This increase in stomatal frequency of leaf also might have resulted in an increase in g_s with increase in the light intensity (Lee et al., 2007). However, high PPFD of 550 μmol m^{-2} s^{-1} decreased the stomatal frequency, which was, we presume, a reaction of the young plants to protect the photosynthetic structures from damage due to the high amount of light. The smaller stomatal frequency could restrain photosynthesis rates by increasing diffusive resistance to CO_2 uptake, which might reduce the burden of photosynthetic organs (Lawson et al., 2011).

The present study demonstrated that the PPFD of 300 μmol m^{-2} s^{-1} caused the hightest Pn. From the above, we observed that a tendency of leaf thickness, palisade cells, stomatal frequency and stomatal pore area per unit leaf area was similar to the activity of Pn. According to Evans (1989) and Goncalves et al. (2008), the greater photosynthetic capacity is often related to higher leaf thickness and palisade cells, which is enhanced by ambient irradiance. In addition, higher stomatal frequency could facilitate CO_2 uptake and thus maintain a high photosynthetic activity (Chartzoulakis et al., 2000). Therefore, we presume the enhancement of Pn due to 300 μmol m^{-2} s^{-1} seems to be concerned with well-developed structure of mesophyll tissue cells, higher stomatal frequency and stomatal area per unit leaf area in leaves.

5. Conclusion

Our results clearly demonstrate that, compared to other light treatments, from 300 to 450 μmol m^{-2} s^{-1}, the biomass and heath index of young plants were better. Meanwhile, the mesophyll tissue, palisade cells and spongy cells in the leaves were thicker, and the stomatal frequency and stomatal area per unit leaf area were higher. More important, 300 μmol m^{-2} s^{-1} induced the highest energy efficiency and activity of Pn. In our research, we found that there was no substantial gain from a PPFD above 300 μmol m^{-2} s^{-1}. Based on the purpose of high efficiency and energy saving, compared to other light treatments, 300 μmol m^{-2} s^{-1} was fit for the culture of young tomato plants.

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