Effects of supplemental lighting to a lower leaf using light-emitting diodes with different spectra on the leaf photosynthetic rate in sweet pepper

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Abstract

Intracanopy lighting (IL) is a newly proposed supplemental lighting technique, irradiating lower leaves of plants from light sources placed between plant stands in high-wire grown vegetable production in a greenhouse. Light-emitting diodes (LEDs) are an appropriate light source for IL because of their compactness and low operating temperatures. To take advantage of features of LEDs, which emit light with a narrow band of wavelengths, we investigated short-term effects of spectra on instantaneous photosynthesis and long-term effects on a decrease in photosynthesis during the senescence of irradiated lower leaves of chamber-grown sweet pepper plants. First, the instantaneous photosynthetic rate of each plant’s fifth leaf was measured under white and monochromatic blue, green and red LED lights at a photosynthetic photon flux density (PPFD) of 150 µmol m⁻² s⁻¹. We confirmed that the rate was low under green light. Second, we grew plants for five weeks in five treatments: four treatments with the fifth leaves irradiated with white, blue, green and red LEDs at a PPFD of 150 µmol m⁻² s⁻¹, and one treatment without irradiation. After the treatments, photosynthetic rates of the irradiated leaves were measured to investigate the long-term effects. Measurements were performed at PPFDs of 300 and 1500 µmol m⁻² s⁻¹ with red and blue LEDs, irrespective of the treatments. The lighting treatments seemed to retard the decreases in photosynthetic rates irrespective of the spectra, but stomatal conductance ($g_s$) of the leaves grown under green light tended to be low compared to those measured under the other colors. In addition to the lower instantaneous photosynthesis, green light might have less enhancing effects on the photosynthesis of the irradiated leaves from the viewpoint of long-term effects. Based on these results, we concluded that green LEDs are not appropriate as an IL light source from the viewpoint of single-leaf photosynthesis.

Key words: Intracanopy lighting, Leaf senescence, Light-emitting diode (LED), Photosynthesis, Stomatal conductance ($g_s$).

1. Introduction

Supplemental lighting in high-wire grown vegetable production in a greenhouse increases the fruit yield when the photosynthetic photon flux density (PPFD) of natural light is insufficient for plant photosynthesis (Rodriguez and Lambeth, 1975). Conventionally, high-pressure sodium (HPS) lamps are mounted above the plant canopy for use as supplemental lighting (top lighting: TL). In recent years, however, intracanopy lighting (IL) has been proposed as a new technique for use in supplemental lighting in a high-wire system. In IL, the light sources are placed between the plant stands to irradiate the lower leaves horizontally. Several previous studies have reported that IL increased fruit yields in high-wire grown vegetables compared to TL (Hovi et al., 2004; Gunnlaugsson and Adalsteinsson, 2006; Hovi-Pekkanen et al., 2006; Hovi-Pekkanen and Tahvonen, 2008; Pettersen et al., 2010).

It is expected that IL is superior to TL based upon...
two fundamental premises: instantaneous photosynthesis of whole plants under IL is expected to be enhanced by a) eliminating the loss of supplemental light by reflection from the upper canopy layer (Trouwborst et al., 2010), and b) irradiating the lower leaves, for which photosynthesis is generally limited by the incident PPFD (Trouwborst et al., 2010). In addition to these short-term effects on instantaneous photosynthesis, IL probably has long-term effects on photosynthesis of the lower, irradiated leaves by retarding their leaf senescence. The term “senescence” has been defined as the sequence of biochemical and physiological events in leaves from maturation until death (Smart, 1994). In general, as a leaf expands and matures, light-limited and -saturated rates of photosynthesis of the leaf increase and reach maximum rates when the leaf fully expands (Jurik et al., 1979). Thereafter the light-limited and -saturated rates decrease (Jurik et al., 1979). This decrease in the photosynthetic rates results from decreases in photosynthetic components, such as photosynthetic pigments, enzymes and proteins (Chabot and Hicks, 1982; Gepstein, 1988), and a decrease in stomatal conductance (Willmer and Fricker, 1996). Several reports have described that a high PPFD retards the decrease in the amounts of photosynthetic components, such as chlorophyll, of the leaves (Goldthwaite and Laetsch, 1967; Thimann et al., 1977; Biswal and Biswal, 1984; Okada et al., 1992). These reports suggest that IL will maintain the photosynthetic rates of the lower leaves by retarding the leaf senescence. Therefore, because of its short- and long-term enhancing effects on photosynthesis, IL is expected to increase whole plant photosynthesis.

The IL light source requires two fundamental characteristics. First, the light source must be compact to be installed between the plant stands. Second, the light source temperature must be low during operation. Thereby it neither inhibits plant growth and development, nor presents an obstacle to greenhouse workers. Conventional HPS lamps cannot fulfill these requirements, but because of their compactness and low operating temperature, light-emitting diodes (LEDs) are an appropriate light source for IL (Trouwborst et al., 2010).

A unique feature of LEDs is that they emit light with a narrow band of wavelengths. Short-term effects of the spectra on instantaneous photosynthesis have been well researched. Reportedly, the action spectrum, absorbance and quantum yield of irradiated leaves depend on the wavelength (McCree, 1972; Inada, 1976), which engenders differences in photosynthetic rates among the spectra irradiated. From the perspective of long-term effects of the spectra, a few studies have investigated the effects on leaf senescence. Red light retards the decrease in chlorophyll a in cotyledons and primary leaves of mustard compared to far-red light (Biswal et al., 1982). Compared to the short-term effects, the long-term effects of the spectra on leaf senescence remain unclear.

These reports describing the short- and long-term effects of spectra suggest the possibility that both short- and long-term photosynthesis can be enhanced by selecting an appropriate spectrum of the light source of IL. To date, however, no attempt has been made to investigate the effects of spectra of IL on the photosynthesis of the irradiated leaves, and no fundamental guideline exists for the spectra of the LEDs for IL. Enhancement of the instantaneous photosynthesis and retardation of leaf senescence by lighting with a specific spectrum might engender a long-term increase in the photosynthesis of the irradiated leaves.

The main issues addressed in this paper are the effects of the spectra a) on instantaneous photosynthesis, and b) on the decrease in photosynthetic rates of the lower irradiated leaves of sweet pepper. Sweet pepper cultivars bearing non-pungent large fruit are a representative vegetable grown in a greenhouse with a high-wire system where IL could be employed for improving fruit productivity. Therefore, one of the cultivars was used as a model in this study. There have been some reports which refer to the effects of supplemental lighting (Fierro et al., 1994; Demers and Gosselin, 1998) and IL (Hovi-Pekkanen et al., 2006) on the fruit yield of sweet pepper. We measured the gas-exchange rates of leaves under white and monochromatic blue, green and red LED light to investigate the effects on the instantaneous photosynthesis. We also measured the gas-exchange rates of leaves that were irradiated with LED lights for five weeks, and investigated the decrease in the photosynthetic rates. Based on these results, we attempted to propose an appropriate spectrum for IL for sweet pepper in terms of leaf photosynthesis.
2. Materials and Methods

2.1 Instantaneous photosynthesis measurements under LEDs with different spectra

Sweet pepper (Capsicum annuum L., cv. Special), a cultivar bearing red fruit, was used as the plant material. Seeds were sown into a plug tray filled with a commercial substrate (Best Mix; Nippon Rockwool Corp., Tokyo, Japan). Seeds were germinated and grown in a temperature-controlled room equipped with white fluorescent tubes (FLR110H-N/A/100; Toshiba Lighting and Technology Corp., Kanagawa, Japan). The seedlings were irradiated with the fluorescent tubes at a PPFD of 150 ± 50 μmol m⁻² s⁻¹ at the tops of plants. The room was maintained at 25 ± 2°C during the 16 h photoperiod and at 20 ± 2°C during the 8 h dark period. On day 17 after sowing, each of the seedlings was transplanted to a 1-L polyethylene pot filled with the same substrate. Plants were watered until germination and were supplied with 50-150 mL of a commercial nutrient solution (Otsuka House Prescription, Otsuka Agritechno Co., Ltd., Tokyo, Japan) at an electrical conductivity (EC) of 1.3 ± 0.1 dS m⁻¹ after germination once daily or every other day.

Gas-exchange rates of fully expanded fifth leaves were measured under white, blue, green and red LED (OSPW5161P, WL; OSUB5161P, BL; OSPG5161P, GL and OSHR5161P, RL; OptoSupply Ltd., Hong Kong, China; Fig. 1) lights on day 35 or 36. Measurements were performed by using a portable gas-exchange measurement system (LI-6400; Li-Cor Inc., Lincoln, NE, USA) in the room. The leaf was sandwiched with a 6-cm² leaf cuvette and its gas-exchange rates were measured at a leaf temperature of 24-27°C, a leaf-to-air vapor pressure deficit of 1.2 ± 0.2 kPa, and a PPFD of 150 μmol m⁻² s⁻¹. Each measurement was performed at two CO₂ concentrations: 1) an atmospheric CO₂ concentration (Cₐ) of 370 ± 10 μmol mol⁻¹, and 2) an intercellular CO₂ concentration (Cᵢ) of 200 ± 3 μmol mol⁻¹. Cᵢ was calculated according to von Caemmerer and Farquhar (1981). It took approximately 20-50 min for the gas-exchange parameters to reach their steady-state values.

2.2 Photosynthesis measurements before and after LED lighting treatments

Sweet pepper seeds were sown, germinated, and grown in a temperature-controlled room until 21 d after seeding, as described above (2.1) except that the photoperiod and dark period were 12 h. On day 21, each of the seedlings was transplanted to the 1-L polyethylene pot, and moved to one of three environmentally controlled growth chambers (MIR-533; Sanyo Electric Co., Ltd., Osaka, Japan) equipped with white fluorescent tubes (FPL55EX-L; Panasonic Inc., Osaka, Japan). The seedlings were irradiated with the fluorescent tubes at a PPFD of 300 ± 50 μmol m⁻² s⁻¹ at the tops of the plants. The chambers were maintained at 25 ± 1°C during the 12 h photoperiod and at 20 ± 1°C during the 12 h dark period. Ambient air was introduced into each chamber using an air pump (DA-60D; ULVAC Inc., Kanagawa, Japan). Six plants were first grown in each chamber. They were thinned to four plants on day 42.

The five treatments consisted of four LED lighting treatments of WL (the leaf was irradiated with white LEDs), BL (blue LEDs), GL (green LEDs), and RL
and a treatment without LED irradiation (NL: not irradiated with LED). From day 42, the fifth leaves in the four LED lighting treatments were irradiated with LED panels at a PPFD of 150 ± 50 µmol m$^{-2}$ s$^{-1}$ during the 12 h photoperiod synchronized to that of fluorescent tubes (Fig. 2). Each panel consisted of a single kind of 60 LEDs that were identical to those used for instantaneous photosynthesis measurements (2.1, Fig. 1). In previous studies, low PPFDs of IL added to TL, approximately 100 µmol m$^{-2}$ s$^{-1}$ or lower, increased fruit yield in sweet pepper (Hovi-Pekkanen et al., 2006) and in cucumber (Hovi et al., 2004; Hovi-Pekkanen and Tahvonen, 2008). The PPFD on the leaf surface in our experiments was determined to be feasible and potentially effective for IL with LEDs. The fifth leaves of NL were shaded by upper leaves from fluorescent tubes. The incident PPFD on the surface of NL leaves measured on day 80 was 50 µmol m$^{-2}$ s$^{-1}$ or lower. We investigated 1) the effects of spectra by comparing the four LED lighting treatments, and 2) the effects of PPFDs by comparing the four LED lighting treatments and the NL. The positional relation between an LED panel and a leaf was adjusted once daily or every other day to maintain PPFD on the leaf. Because of the limited space, the experiment was repeated four times, each comparing three treatments of NL and two out of four LED lighting treatments: NL, RL and BL were applied for the first experiment, NL, WL and GL for the second, NL, BL and WL for the third, and NL, GL and RL for the fourth.

Gas-exchange rates of the fifth leaves were measured before the treatments (between days 38 and 40) in the third experiment. Measurements were performed as described above (2.1) except that light was provided from red and blue LEDs (6400-02B; Li-Cor Inc., Lincoln, NE, USA) at a PPFD of 1500 µmol m$^{-2}$ s$^{-1}$ and a $C_i$ of 200 ± 3 µmol mol$^{-1}$. Measurements of the rates after the treatments (between days 74 and 80) were performed in order to assess the effects on leaf senescence. The measurements were performed at PPFDs of 300 and 1500 µmol m$^{-2}$ s$^{-1}$ with the red and blue LEDs and at a $C_o$ of 370 ± 10 µmol mol$^{-1}$ in the first and second experiments, or at a $C_i$ of 200 ± 3 µmol mol$^{-1}$ in the third and fourth experiments.

2.3 Statistical analysis

Significant differences between measurement periods were tested using Welch’s t-test, and those among treatments were tested using one-way analysis of variance (ANOVA) followed by Fisher’s least significant difference (LSD) test, respectively. All statistical analyses were performed using statistical software R ver. 2.13.1 (R Development Core Team, 2011).

3. Results and Discussion

3.1 Instantaneous photosynthesis under LEDs with different spectra

Instantaneous net photosynthetic rate measured under GL at a $C_o$ of 370 µmol mol$^{-1}$ and a PPFD of 150 µmol m$^{-2}$ s$^{-1}$ was significantly lower than the rates measured under WL, BL and RL (Fig. 3). No significant differences were found in the stomatal conductance ($g_s$) and $C_i$ among the leaves of the four treatments (Table 1). Instantaneous net photosynthetic rate measured at a $C_i$ of 200 µmol mol$^{-1}$ and a PPFD of 150 µmol m$^{-2}$ s$^{-1}$ presented a similar tendency to that measured at a constant $C_o$, i.e., lower under GL than under the other LED lights (data not shown). The absorptance of plant leaves is reported to be lower under green light compared to that under blue and red lights (McCree, 1972; Inada, 1976). The lower photosynthetic rates under GL observed in our measurements are expected to result from this lower absorptance.

3.2 Net photosynthetic rates measured before and after five weeks

Net photosynthetic rate measured between days 38
and 40 was significantly higher than that measured between days 74 and 80 (Table 2). Thus, we confirmed that the fifth leaves were in the senescing stage during the five weeks under the conditions of this study. We therefore discuss the effects of LED lighting treatments on leaf senescence by focusing on photosynthesis after the 5-week treatments in the following sections.

Table 2. Net photosynthetic rates of fifth leaves measured between days 38 and 40, and between days 74 and 80. Measurements were made at an intercellular CO2 concentration of 200 µmol mol⁻¹ and a PPFD of 1500 µmol m² s⁻¹.

<table>
<thead>
<tr>
<th>Days after germination</th>
<th>Net photosynthetic rate [µmol CO₂ m⁻² s⁻¹]</th>
</tr>
</thead>
<tbody>
<tr>
<td>38-40</td>
<td>10.4 ± 1.1*</td>
</tr>
<tr>
<td>74-80</td>
<td>4.5 ± 0.6</td>
</tr>
</tbody>
</table>

Means ± standard errors were shown (n=7). An asterisk (*) represents a significant difference by Welch’s t-test between the two measurement periods (P<0.05).

3.3 Photosynthesis at a constant C₅ after LED lighting treatments

Net photosynthetic rates measured at a C₅ of 370 µmol mol⁻¹ and a PPFD of 300 µmol m² s⁻¹ of RL- and BL-leaves were significantly higher than that of NL-leaves (Fig. 4A). No significant differences were found among the rates of NL-, WL- and GL-leaves (Fig. 4B). No significant differences were found in the gₛ and C₅ among NL-, RL- and BL-leaves or among NL-, WL- and GL-leaves (Table 3). Therefore, the higher photosynthetic rates of RL- and BL-leaves than that of NL-leaves were not attributable to the higher extent of stomatal opening. A possible cause of the higher photosynthetic rates of RL- and BL-leaves than that of NL-leaves is their higher contents of photosynthetic light-harvesting components responsible for light-limited photosynthesis. For instance, the loss of chlorophyll, light-harvesting photosynthetic pigment, was reported to be delayed by light irradiation (Goldthwaite and Laetsch, 1967; Thimann et al., 1977; Biswal and Biswal, 1984; Okada et al., 1992). Not only PPFDs, but also spectra could affect the loss. Red (Mishra and Pradhan, 1973; Okada et al., 1992; Biswal and Choudhury, 1986) and blue (Biswal and Choudhury, 1986) lights have been reported to retard chlorophyll loss of the irradiated leaves. In our experiments, however, the effects of spectra between RL- or BL-leaves and WL- or GL-leaves were not compared. Thus, we cannot make a clear decision on the effects of the spectra on chlorophyll loss based on the results.

Among the leaves of the LED lighting treatments, no
significant differences were found between RL- and BL-leaves or WL- and GL-leaves in the photosynthetic rates, $g_s$ and $C_i$ (Figs. 4A and 4B, Table 3).

Net photosynthetic rates measured at a $C_a$ of 370 µmol mol$^{-1}$ and a PPFD of 1500 µmol m$^{-2}$ s$^{-1}$ of RL- and WL-leaves were significantly higher than those of NL-leaves respectively (Figs. 4C and 4D). The photosynthetic rates of BL- and GL-leaves also tended to be higher than those of NL-leaves, though not significantly (Figs. 4C and 4D). The $g_s$ of WL-leaves was higher than that of NL-leaves, although the $C_i$ of the leaves of the four LED lighting treatments were lower than those of NL-leaves (Table 3). Generally, a higher $C_i$ engenders a higher rate of light-saturating photosynthesis (Farquhar et al., 1980; von Caemmerer and Farquhar, 1981). Under light-saturated and CO$_2$-limited conditions, photosynthetic rates of leaves are limited by the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), a key enzyme in CO$_2$ fixation, and CO$_2$ diffusion from atmosphere to chloroplast stroma (von Caemmerer and Farquhar, 1981). The leaves of the LED lighting treatments can have higher activity of Rubisco and/or higher internal CO$_2$ conductance from intercellular space to stroma, which might explain the higher photosynthetic rates despite the lower $C_i$.

From the viewpoint of comparison among the LED lighting treatments, the photosynthetic rate of GL-leaves measured at a PPFD of 1500 µmol m$^{-2}$ s$^{-1}$ was significantly lower than that of WL-leaves (Fig. 4D).

**Table 3.** Stomatal conductance ($g_s$) and intercellular CO$_2$ concentrations ($C_i$) of fifth sweet pepper leaves measured after 5-week LED lighting treatments (the leaves were irradiated with white (WL), blue (BL), green (GL) and red LED (RL) lights at a PPFD of 150 µmol m$^{-2}$ s$^{-1}$, and not irradiated (NL)). Measurements were made at an atmospheric CO$_2$ concentration of 370 µmol mol$^{-1}$ and at PPFDs of 300 and 1500 µmol m$^{-2}$ s$^{-1}$.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>$g_s$ [mol m$^{-2}$ s$^{-1}$]</th>
<th>$C_i$ [µmol mol$^{-1}$]</th>
<th>$g_s$ [mol m$^{-2}$ s$^{-1}$]</th>
<th>$C_i$ [µmol mol$^{-1}$]</th>
</tr>
</thead>
<tbody>
<tr>
<td>NL</td>
<td>0.25 ± 0.04$^a$</td>
<td>321.1 ± 3.5$^a$</td>
<td>0.27 ± 0.05$^a$</td>
<td>319.2 ± 3.5$^a$</td>
</tr>
<tr>
<td>RL</td>
<td>0.21 ± 0.05$^a$</td>
<td>290.4 ± 9.8$^a$</td>
<td>0.33 ± 0.06$^a$</td>
<td>289.5 ± 0.4$^b$</td>
</tr>
<tr>
<td>BL</td>
<td>0.24 ± 0.05$^a$</td>
<td>297.5 ± 11.7$^a$</td>
<td>0.27 ± 0.07$^a$</td>
<td>277.6 ± 11.0$^b$</td>
</tr>
<tr>
<td>WL</td>
<td>0.11 ± 0.02$^a$</td>
<td>270.8 ± 12.5$^a$</td>
<td>0.19 ± 0.02$^b$</td>
<td>293.6 ± 5.3$^a$</td>
</tr>
<tr>
<td>GL</td>
<td>0.10 ± 0.02$^a$</td>
<td>248.1 ± 7.9$^a$</td>
<td>0.19 ± 0.02$^b$</td>
<td>271.6 ± 4.1$^b$</td>
</tr>
</tbody>
</table>

Means ± standard errors were shown (n=3–4).

Different small letters represent significant differences by LSD tests among treatments ($P<0.05$).
The lower photosynthetic rate of GL-leaves might result from the lower activity of the photosynthetic components related to the light-saturated photosynthetic rates like Rubisco, or their lower \( g_s \), and associated relative lower \( C_i \) than that of WL-leaves (Table 3). No significant difference was found between the rates of RL- and BL-leaves (Fig. 4C).

### 3.4 Photosynthesis at a constant \( C_i \) after LED lighting treatments

Net photosynthetic rates measured at a constant \( C_i \) reflected both effects of \( C_i \) and possibly the amounts of the photosynthetic components of the leaves. To eliminate the effects of \( C_i \), measurements were performed at a constant \( C_i \) of 200 \( \mu \text{mol} \) mol\(^{-1} \).

Net photosynthetic rates of BL- and WL-leaves at a \( C_i \) of 200 \( \mu \text{mol} \) mol\(^{-1} \) and a PPFD of 300 \( \mu \text{mol} \) m\(^{-2} \) s\(^{-1} \) tended to be higher than that of NL-leaves, although the differences were not statistically significant (Fig. 5A). The rates of GL- and RL-leaves were significantly higher than that of NL-leaves (Fig. 5B). Consequently, the photosynthetic rates of the leaves of the LED lighting treatments tended to be higher than those of NL-leaves. These higher photosynthetic rates of the leaves of the LED lighting treatments imply that the LED lighting treatments retarded decreases in the photosynthetic components, thereby limiting the light-limited rate of photosynthesis.

However, among the LED lighting treatments, no significant differences were found between BL- and WL-leaves or between GL- and RL-leaves in the photosynthetic rates measured at a PPFD of 300 \( \mu \text{mol} \) m\(^{-2} \) s\(^{-1} \) (Figs. 5A and 5B).

The photosynthetic rate of GL-leaves measured at a \( C_i \) of 200 \( \mu \text{mol} \) mol\(^{-1} \) and a PPFD of 1500 \( \mu \text{mol} \) m\(^{-2} \) s\(^{-1} \) was higher than that of NL-leaves (Fig. 5C). The BL-, WL- and RL-leaves’ rates of photosynthesis tended to be higher than those of NL-leaves, but they were not significant (Figs. 5C and 5D). These results suggest that the LED lighting treatments retarded the decrease in the photosynthetic components related to the light-saturated rate of photosynthesis (e.g., Rubisco) compared to NL. The amount of Rubisco, which serves as a \( \text{CO}_2 \)-fixing enzyme, is reported to be affected by the PPFDs of the growth environment (Seemann et al., 1987; Hikosaka, 1996).

Among the LED lighting treatments in the photosynthetic rates measured at PPFD of 1500 \( \mu \text{mol} \) m\(^{-2} \) s\(^{-1} \), no significant differences were found between BL- and WL-leaves or GL- and RL-leaves (Figs. 5C and 5D), which implies that the leaves of LED lighting treatments represented the same degree of activity of photosynthetic components limiting photosynthesis under a saturated PPFD, e.g., Rubisco. Looking back over the results of the photosynthetic rates measured at a constant \( C_a \) (Fig. 4D), this result supports our latter inference that a lower photosynthetic rate of GL leaves resulted from the lower \( g_s \) and associated lower \( C_i \), not from the lower amounts of the photosynthetic components. The low \( g_s \) of GL-leaves observed in our experiment (Table 3) suggests the possibility that a leaf senescing under green light has a lower degree of \( g_s \). Some reports infer that green light irradiation inhibits stomatal opening (Frechilla et al., 2000; Talbott et al., 2002). However, these are short-term effects within several minutes to an hour. Further work on the long-term effects of the spectra on the stomatal opening...
needs to be conducted.

3.5 Proposing appropriate spectra of the light source in IL

Considering the short-term effects on photosynthesis of an irradiated leaf, instantaneous net photosynthetic rate measured under GL was significantly lower than those measured under WL, BL and RL (Fig. 3), as reported previously (McCree, 1972; Inada, 1976). It is apparent that green light might not be appropriate to the light source of IL with the object of increasing instantaneous photosynthesis of the lower irradiated leaves.

Regarding the long-term effects, when comparing the leaves of the LED lighting treatments and NL-leaves in net photosynthetic rates, the rates of the irradiated leaves tended to be higher than those of NL-leaves, irrespective of CO₂ concentrations and PPFDs (Figs. 4 and 5). These results suggest that the LED lighting treatments retarded the leaf senescence and caused an increase in the photosynthetic rates of the lower irradiated leaves in sweet pepper. This increase of the photosynthetic rates may contribute to increasing fruit yield, as previously reported in cucumber (Hovi et al., 2004; Hovi-Pekkanen and Tohvanen, 2008; Pettersen et al., 2010), in tomato (Gunnlaugsson and Adalsteinsson, 2006), and in sweet pepper (Hovi-Pekkanen et al., 2006).

However, in the long-term effects of the spectra, no significant differences were found between the LED lighting treatments except that the photosynthetic rate of GL-leaves measured at a constant Cᵣ and a PPFD of 1500 µmol m⁻² s⁻¹ was significantly lower than that of WL-leaves (Fig. 4D). A likely cause of the lower photosynthetic rate is lower gₛ of GL-leaves (Table 3). Therefore, comparison among LED lighting treatments suggests that 1) the spectra have little effect on a decrease in the photosynthetic components of the irradiated leaves, and 2) green light possibly has a long-term effect of inhibiting stomatal opening of the irradiated leaves.

As a result, we can infer that the LED lighting treatment increases instantaneous photosynthesis and retards leaf senescence of irradiated leaves, irrespective of the spectra. Consequently, the treatments might increase the photosynthesis of the irradiated leaves. When it comes to a comparison among the spectra of the irradiated light, the instantaneous photosynthetic rate was lower under green LED light than under white, blue and red LED lights. In addition, from the viewpoint of long-term effects on leaf senescence, green LED light might have less effect on enhancing photosynthesis of the irradiated leaves. Based on these results, we concluded that green LEDs are not appropriate as IL light sources for sweet pepper from the viewpoint of single-leaf photosynthesis.

Regulating leaf senescence can play a key role in photosynthetic properties not only of irradiated leaves but also of other parts of leaves that are not irradiated directly. Trouwborst et al. (2010) reported that photosynthesis of upper leaves was inhibited when lower leaves were irradiated with LEDs and retarded from senescence. Consequently, considering photosynthesis of the whole plant, it might not always be beneficial to retard the senescence of the lower irradiated leaves with IL. More research is necessary to elucidate the photosynthetic characteristics of the upper, non-irradiated leaves, when the lower leaves are irradiated.

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References


