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Effect of green light wavelength and intensity on photomorphogenesis and photosynthesis in *Lactuca sativa*

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ABSTRACT

In this study, the effects of green light-emitting diodes (LEDs) with different peak wavelengths and light intensities on lettuce growth and photosynthesis were evaluated. The green LEDs used were G510 (peak wavelength: 510 nm; band width at half peak height: 18 nm), G520 (524 nm; 30 nm) and G530 (532 nm; 36 nm) at a photosynthetic photon flux (PPF) of 100, 200 and 300 μmol m^{-2} s^{-1}, respectively (maximum output of G530 was PPF 260). Shoot and root growth in lettuce plants irradiated with green LED light at PPF 100 decreased compared with white fluorescent light, but root growth of plants irradiated with green LED light at PPF 200 increased, and shoot growth of plants grown under G510 at PPF 300 was the highest of all light sources. Leaf photosynthetic rate (Pn) of plants irradiated with green LED light at PPF 200 was dramatically higher than that at PPF 100, and the Pn of plants irradiated with G510 was the highest of all light sources. These results indicated that high-intensity green LED light was effective to promote plant growth and, in particular, short-wavelength green light was available for active plant growth.

1. Introduction

Plants appear green because green light is reflected by the plant. Therefore, green light has been thought to be of no use for plant growth, particularly for photomorphogenesis and photosynthesis. Plants grow normally under sunlight or combined artificial red and blue light (Kim et al., 2004a; Ohasi-Kaneko et al., 2007), but irradiation with green light induces stem elongation (Folta, 2004) and decreased biomass production (Folta and Maruhnich, 2007). Green light is absorbed only weakly by chlorophylls and pigments extracted from green leaves (Terashima et al., 2009). However, Terashima et al. (2009) indicated that green light mixed with strong white light drove photosynthesis more effectively than red light in sunflower leaves. Thus, green light is often held to be unavailable for plant growth, but might be available for plant growth under strong light intensity.

Green higher plants utilize chlorophylls a and b and a variety of carotenoids to capture light for photosynthesis (Nishio, 2000). The percentage absorption of blue or red light by plant leaves is about 90% and that of green light is about 70–80% (Terashima et al., 2009). Thus, plant development and physiology are strongly influenced by blue or red light. Blue light suppresses hypocotyl elongation and induces biomass production, and red light induces hypocotyl elongation and expansion in leaf area (McNellis and Deng, 1995; Johkan et al., 2010). Green light also affects plant morphology and physiology, including leaf growth, stomatal conductance and early stem elongation (Folta, 2004; Kim et al., 2004a,b).

Plant growth under the combination of blue and red light has been studied in lettuce, spinach, komatsuna (Japanese mustard spinach) and radish (Yorio et al., 2001; Hanyu and Shoji, 2002; Ohasi-Kaneko et al., 2007). The combination of red and blue light was an effective lighting source to produce plant biomass, and the addition of green light with blue and red light was also effective (Kim et al., 2004a,b). Green light can penetrate into the plant canopy better than blue or red light (Klein, 1992). Leaves in the lower canopy would be able to use the transmitted green light in photosynthesis (Nishio, 2000), so plant growth is promoted by the addition of green light with blue and red light (Kim et al., 2004a,b). However, the growth of plants irradiated with green light decreases as the proportion of green light increases (Kim et al., 2004a,b).

Plant physiological reactions to green light and the effects of green light on plant growth have been investigated, but there is no report of plants being cultivated under green light only. Hence, the question arises whether the plants could be grown under green light only. Major previous reports showed that green light was not active for plant growth (Van et al., 1977; Kim et al., 2004a,b), and some previous reports showed that green light was active for plant growth when the proportion of green light to photosynthetic

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photon flux (PPF) was low (Kim et al., 2004a,b; Terashima et al., 2009). Terashima et al. (2009) reported that sufficient blue or red lights were strongly absorbed near the adaxial side of leaf, but sufficient green light, which chloroplasts are hard to absorb, penetrated and was absorbed by the chloroplasts in the abaxial side. However, typical values of absorptance at 550 nm range from 50% in lettuce (Inada, 1976). We thought that low activation of plant growth with the green light due to the lower PPF of light source in the previous works. Therefore, previous reports raise the hypothesis that the green light with higher PPF would penetrate into the plant leaves, be absorbed in chloroplast and drive the photosynthesis enough to growth. Moreover, the green light region is between 500 and 600 nm, but it is unknown which particular wavelengths of green light promote plant growth. In this study, three types of green light-emitting diode (LED) lights with different peak wavelengths and light intensities were used to investigate the effect of green light on lettuce growth and photosynthesis, and the availability of green light for plant growth is discussed.

2. Materials and methods

2.1. Plant growth

Germinated seeds of red leaf lettuce (*Lactuca sativa* L. cv Banchu Red Fire; Takii Seed Co., Kyoto, Japan) were sown in urethane cubes (W2.4 cm × D2.4 cm × H2.8 cm) filled with water. The seedlings were grown at 23 ± 2 °C under 100 μmol m^{-2} s^{-1} PPF for 14 h with white fluorescent lamps (FL; FLR110H-W1A, Mitsubishi/Osram Co., Kyoto, Japan). The seedlings were supplied with a nutrient solution (pH 5.8), containing 9.2 N, 2.6 P, 4.4 K, 2.2 Ca, and 0.8 Mg (in mmol L^{-1}) 7 d after sowing (DAS). The seedlings were transplanted to cultivated panels, supplied with 1 L nutrient solution until the end of experiments, and cultivated at 25 °C, relative humidity (RH) 60% and 900 μmol mol^{-1} CO_2 in a growth chamber (VB1514, W200 cm × D75 cm × H140 cm; Vötsch, Germany). The plants were irradiated with different light spectra from the green LEDs, namely G510 (peak wavelength: 510 nm; band width at half peak height: 18 nm; ISL-305X302-GGGG505, CCS Co., Kyoto, Japan), G520 (peak wavelength: 524 nm; band width at half peak height: 30 nm; ISL-305X302-GGGG525, CCS) and G530 (peak wavelength: 532 nm; band width at half peak height: 36 nm; ISL-305X302-GGGG525, CCS) 10 DAS. All seedlings were irradiated for 24 h at PPF 100, 200 or 300 μmol m^{-2} s^{-1}, but maximum output of G530 was PPF 260 μmol m^{-2} s^{-1}. The wavelength of the light source was determined with a USB2000 spectrometer (Ocean Optics, Dunedin, FL, USA) (Fig. 1). At 17 DAS, leaf number, third-leaf dimensions (leaf length, leaf width, petiole length, and petiole width), leaf area, fresh weight (FW) and dry weight (DW) were measured.

2.2. Leaf gas exchange

At 17 DAS, photosynthetic rate (Pn) and transpiration rate were determined on the second fully expanded leaf with an Arabidopsis leaf chamber (6400-15 Arabidopsis Chamber, 0.785 cm^2, LI-COR, Lincoln, NE, USA) mounted on an infrared CO_2/H_2O analyzer (LI-6400 Portable Photosynthesis System, LI-COR). The conditions in the measurement chamber were controlled as follows: flow rate, 300 μmol s^{-1}; CO_2 concentration in the sample chamber, 900 μmol mol^{-1}; RH, 60%; air temperature, 25 °C. To measure photosynthetic CO_2 fixation under different light conditions, gas exchange characteristics of the second leaf were determined under the FL, G510, G520 and G530 light sources at PPF 100, 200 and 300 μmol m^{-2} s^{-1}.

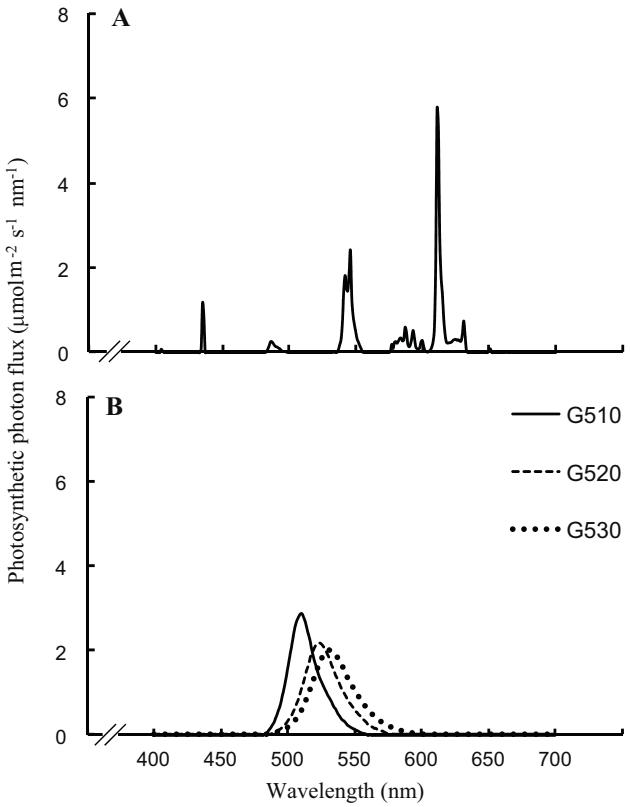

Fig. 1. Spectral photon flux distributions for the lighting treatments. (A) White fluorescent lamp (FL); (B) green light-emitting diodes (LEDs); G510: peak wavelength 510 nm, G520: peak wavelength 524 nm, G530: peak wavelength 532 nm. Total photosynthetic photon flux was 100 μmol m^{-2} s^{-1} in each treatment. Spectral scans of LED light were recorded 20 cm below the panel of LEDs and 45 cm below the FL.

2.3. Statistical analysis

Tukey's multiple range test was used to test the difference between more than two means at the 0.05 significance level using XLSTAT software (Esmi Co., Tokyo, Japan).

3. Results

3.1. Plant growth and morphology

Among plants grown under the FL, the plants irradiated at PPF 100 and 200 showed normal photomorphogenesis, but at PPF 300 the plants were severely dwarfed (Fig. 2). Under green LED light, the plants irradiated at PPF 100 showed succulent growth in contrast to the FL treatment and, moreover, the plants irradiated with G530 at PPF 100 showed remarkably succulent growth. At PPF 200, the plants irradiated with G510 and G520 did not exhibit succulent growth. At PPF 300, the plants irradiated with G510 and G520 were of normal appearance, similar to the plants irradiated with FL at PPF 100. However, the plants irradiated with G530 at PPF 200 and 300 were slightly succulent.

No difference was observed in leaf number irrespective of the wavelength at PPF 100 and 200, but the leaf number of plants irradiated with G510 was significantly increased at PPF 300 (Table 1). The leaf area and FW of plants treated with green LED light were lower than those irradiated with FL at PPF 100, and those grown under the FL at PPF 200 showed maximum leaf area and FW of 65.8 cm^2 and 1738 mg, respectively. However, the leaf area and FW of plants irradiated with G510 at PPF 300 were significantly increased by 71% and 59%, respectively, compared to that at PPF 200. The shoot DW

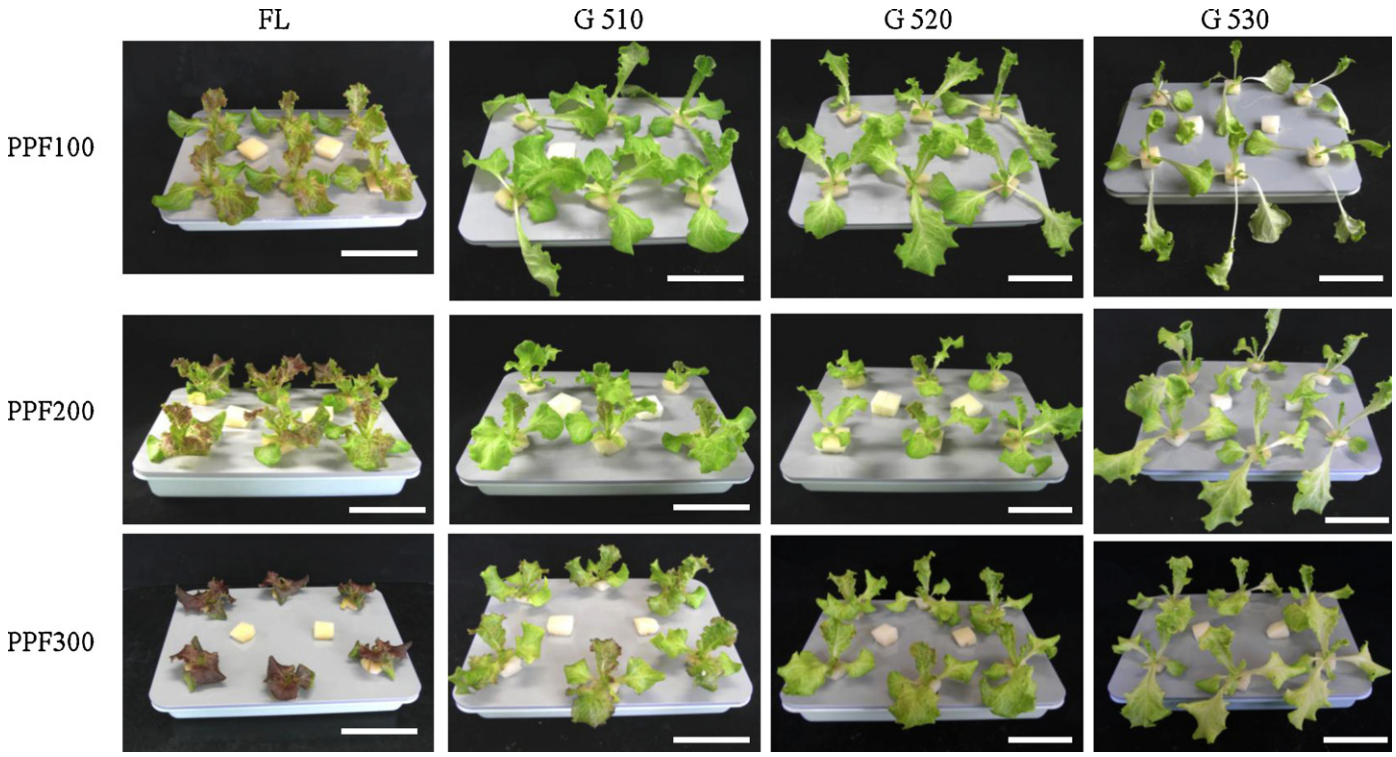

Fig. 2. Morphology of red leaf lettuce plants treated with light from a white fluorescent lamp (FL) and green light-emitting diodes (LED). Peak wavelength for each LED was 510 nm (G510), 524 nm (G520) and 532 nm (G530). Plants were photographed 17 d after sowing. Bars indicate 8 cm. Total photosynthetic photon flux was 100, 200 and 300 μmol m^{-2} s^{-1}. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

of plants treated with green LED light was lower than that with FL at PPF 100 and 200. At PPF 300, the shoot DW of plants treated with G510 at PPF 300 was increased by 83% compared to that at PPF 200. The leaf area, FW and DW of plants treated with G510 at PPF 300 were similar to those of plants irradiated with FL at PPF 100 and 200. The root DW of plants treated with green LED light increased with increasing PPF; the root DW was highest in plants treated with G510 at PPF 300. The shoot/root (S/R) ratio of plants treated with FL increased at PPF 200 and decreased at PPF 300 compared to that of plants at PPF 100, but those treated with green LED light decreased from >4.4 at PPF 100 to <2.5 at PPF 200 and 300 (Fig. 3A). The specific leaf area (SLA) of plants irradiated with FL and G510 decreased with increasing PPF, but those irradiated with G520 and G530 decreased at PPF 200 and increased at PPF 300 (Fig. 3B).

Leaf length, leaf width, petiole length and petiole width were strongly affected by the light intensity (Table 2). The leaf length and width of plants irradiated with green LED light were decreased at PPF 200 and increased at PPF 300, but those irradiated with FL were decreased at PPF 300. At PPF 100, the petiole length in plants irradiated with G510, G520 and G530 elongated 211%, 223% and 331%, respectively, compared to FL. The petiole length was reduced with increasing PPF, but elongated when treated with G530 at PPF 300. The petiole width increased in plants irradiated with G510 and G520 with increasing PPF.

Table 1
Effects of light of different intensities from a white fluorescent lamp and green light-emitting diodes on leaf number, leaf area, fresh weight and dry weight of red leaf lettuce plants after 7 d irradiation.

PPF[a] (μmol m^{-2} s^{-1})	Light source[b]	Leaf number	Leaf area (cm^2)	Fresh weight (mg)	Dry weight (mg, DW)	
					Shoot	Root
100	FL	4.1 a[c]	67.6 a	1633 a	96.9 a	22.2 a
	G510	4.1 a	58.0 a	1526 a	72.8 ab	11.7 b
	G520	4.1 a	58.6 a	1467 a	74.8 ab	11.6 b
	G530	4.0 a	48.8 a	1044 a	53.4 b	12.8 b
200	FL	4.3 a	65.8 a	1738 a	153.0 a	21.0 b
	G510	4.0 a	38.0 b	953 b	76.4 b	32.0 a
	G520	4.0 a	39.2 b	887 b	68.9 b	30.2 ab
	G530	4.2 a	40.6 b	1055 b	66.6 b	30.0 ab
300	FL	4.4 b	38.1 b	900 b	129.8 a	45.3 ab
	G510	5.2 a	65.0 a	1516 a	140.4 a	57.8 a
	G520	4.3 b	63.3 a	1000 b	89.3 b	39.3 ab
	G53O[d]	4.2 b	68.0 a	1076 b	85.7 b	30.8 b

[a] Photosynthetic photon flux.
[b] FL: White fluorescent lamp; G510, G520 and G530: green light-emitting diodes; G510: peak wavelength 510 nm; G520: peak wavelength 524 nm; G530: peak wavelength 532 nm.
[c] Different letters indicate a significance difference within a PPF treatment ($P < 0.05$; Tukey's multiple range test, $n \geq 5$).
[d] PPF was 260 μmol m^{-2} s^{-1}.

Table 2
Effects of light of different intensities from a white fluorescent lamp and green light-emitting diodes on leaf length, leaf width, petiole length and petiole width in red leaf lettuce plants after 7 d irradiation.

PPF[a] (μmol m^{-2} s^{-1})	Light source[b]	Leaf length (mm)	Leaf width (mm)	Petiole length (mm)	Petiole width (mm)
100	FL	52.6 a[c]	59.2 a	19.4 c	3.3 a
	G510	54.0 a	51.2 ab	41.0 b	3.0 a
	G520	58.4 a	53.3 ab	43.3 b	3.0 a
	G530	52.6 a	40.4 b	64.3 a	1.9 b
200	FL	55.8 a	60.2 a	14.7 a	4.2 a
	G510	41.3 b	42.3 b	18.0 a	3.5 b
	G520	44.7 b	43.1 b	21.2 a	3.3 b
	G530	49.5 ab	42.2 b	23.8 a	3.1 b
300	FL	37.6 c	45.7 b	7.2 c	3.6 be
	G510	50.5 b	59.5 a	14.0 b	4.3 a
	G520	46.7 b	53.8 ab	14.6 b	4.4 a
	G530[d]	67.5 a	57.4 a	30.7 a	3.9 ab

[a] Photosynthetic photon flux.
[b] FL: White fluorescent lamp; G510, G520 and G530: green light-emitting diodes; G510: peak wavelength 510 nm; G520: peak wavelength 524 nm; G530: peak wavelength 532 nm.
[c] Different letters indicate a significance difference within a PPF treatment ($P < 0.05$; Tukey's multiple range test, $n \geq 5$).
[d] PPF was 260 μmol m^{-2} s^{-1}.

3.2. Photosynthesis and transpiration

At PPF 100, the second-leaf Pn of plants irradiated with green LED light was lower than that with FL. At PPF 200 and 300, the Pn of plants irradiated with green LED light drastically increased from that at PPF 100, and the Pn of plants irradiated with G510 (13.6 μmol CO_2 m^{-2} s^{-1}) was the highest recorded in all light treatments (Fig. 4A). Transpiration rates of the second leaf in plants irradiated with FL were higher than those of plants treated with green LED light (Fig. 4B). Of the latter, the transpiration rate of plants irradiated with G510 was higher than those treated with G520 and G530.

4. Discussion

The green LED light used in this study had peak wavelengths at 510, 520 and 530 nm. Although the difference in peak wavelength among the green LEDs was only 10 nm, lettuce plants showed

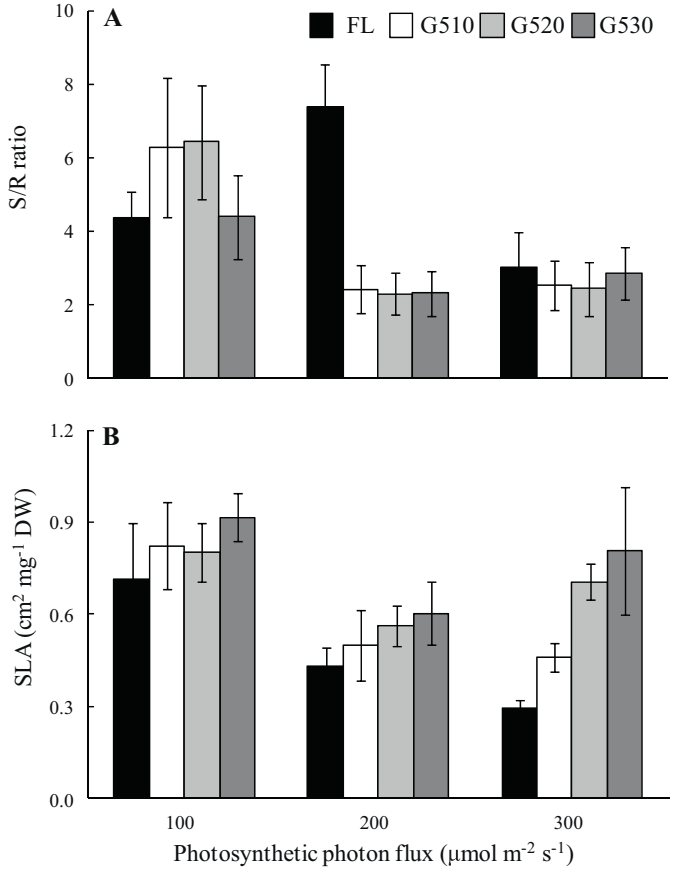

Fig. 3. Effects of the light intensity and spectral composition of green light-emitting diodes on shoot/root (S/R) ratio and specific leaf area (SLA) in red leaf lettuce plants after 7 d irradiation. FL: White fluorescent lamp, G510: peak wavelength 510 nm, G520: peak wavelength 524 nm, G530: peak wavelength 532 nm.

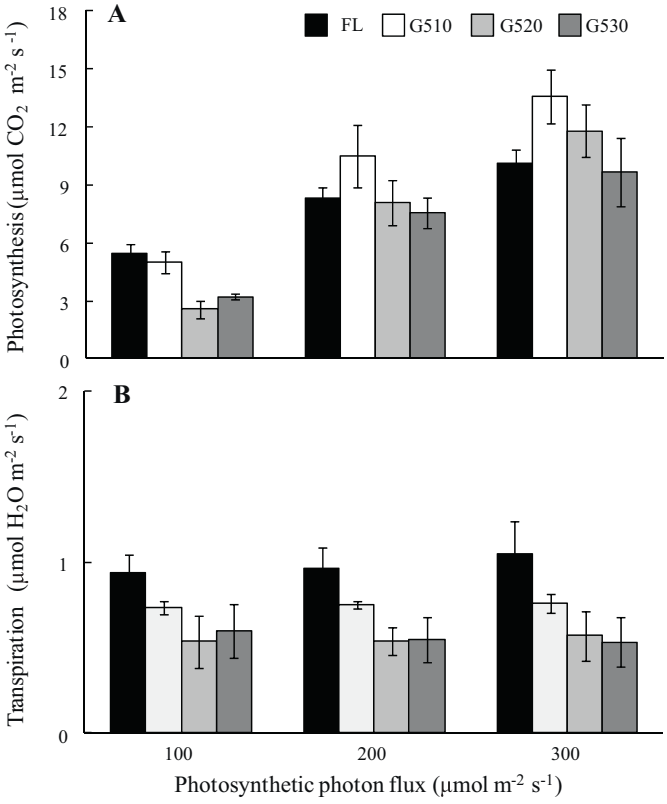

Fig. 4. Effects of the light intensity and spectral composition of green light-emitting diodes on photosynthesis and transpiration rates in the second leaf of red leaf lettuce plants after 7 d irradiation. FL: White fluorescent lamp, G510: peak wavelength 510 nm, G520: peak wavelength 524 nm, G530: peak wavelength 532 nm.

Table 3
Spectral data for the white fluorescent lamp and the green light-emitting diodes G510, G520 and G530 at PPF 100 and 300 μmol m^{-2} s^{-1}.

PPF[a] (μmol m^{-2} s^{-1})	Light source[b]	Photon flux (μmol m^{-2} s^{-1})			
		400–449 nm	450–499 nm	500–549 nm	550–599 nm
100	FL	4.2	3.3	27.7	13.9
	G510	0.0	10.8	88.2	1.0
	G520	0.0	1.9	89.7	8.4
	G530	0.0	1.0	78.5	20.5
300	FL	13.2	7.7	87.5	42.3
	G510	0.0	46.0	253.5	0.5
	G520	0.0	6.4	274.2	19.4
	G530[c]	0.0	0.2	218.7	41.1

[a] Photosynthetic photon flux.
[b] FL: White fluorescent lamp; G510, G520 and G530: green light-emitting diodes; G510: peak wavelength 510 nm; G520: peak wavelength 524 nm; G530: peak wavelength 532 nm.
[c] PPF was 260 μmol m^{-2} s^{-1}.

distinct growth responses to irradiation with each LED. At PPF 100, green LED light promoted leaf elongation compared to FL, and the leaf length of plants irradiated with G530 was longer than that with G510. Thus, leaf elongation was stimulated by long-wavelength green light. Folta (2004) reported that green light promoted early stem elongation that antagonizes growth inhibition. In addition, lettuce plants grown under G530 showed succulent growth. Plant development is strongly influenced by light quality (McNellis and Deng, 1995; Johkan et al., 2010). Blue light, which has a short wavelength, suppressed stem elongation, whereas red light, which has a long wavelength, promoted stem and leaf elongation. The difference in peak wavelength between G510 and G530 was only 20 nm, but the effect on leaf elongation was greater at the longer wavelength than at the shorter wavelength. The significant elongation of the petiole in plants irradiated with G530 at PPF 260 (Table 2) might also be affected by the long wavelength.

Kim et al. (2004a) reported that shoot growth in lettuce plants irradiated with cool-white fluorescent (CWF) light was higher than that with green fluorescent (GF) light at the same PPF. The SLA of lettuce plants irradiated with CWF was lower than that with GF. The green photon flux in CWF and GF was 76 and 129 μmol m^{-2} s^{-1}, respectively (total photon flux was 150 μmol m^{-2} s^{-1}). Their report indicated that a high percentage of green light in the light source suppressed plant growth. In the present study, shoot and root growth of lettuce plants irradiated with green LED light at PPF 100 also decreased compared with FL. However, root growth of plants irradiated with green LED light at PPF 200 increased compared with FL and shoot growth in plants treated with G510 at PPF 300 was the highest in all of the treatments. Moreover, S/R ratios of lettuce plants irradiated with green light at PPF 200 and 300 were lower than those at PPF 100. Therefore, green light with high PPF was indicated to stimulate root growth in lettuce plants.

The single-leaf photosynthetic rate of lettuce plants irradiated with green LED light at PPF 100 was lower than that with FL, but at high light intensity, such as PPF 200 and 300, Pn of plants irradiated with G510 was higher than that with FL. Terashima et al. (2009) reported that in moderate to strong white light, green light drove photosynthesis more effectively than red light. Green light was reflected from the plant surface, but penetrated green light drove photosynthesis with high efficiency (Björkman, 1968; Balegh and Biddulph, 1970; McCree, 1972; Inada, 1976; Terashima et al., 2009). Moreover, the SLA of lettuce plants irradiated with G510 was lower than those of G520 and G530. Since light absorption by the leaf surface and reflection within the leaf increase roughly in proportion to leaf thickness, the drastic increase in Pn of the lettuce plants irradiated with G510 at PPF 200 might also reflect leaf thickness.

At PPF 100, the Pn of lettuce plants irradiated with FL and G510 was almost the same, but the DW with FL was higher than that with G510. Kim et al. (2004a) reported that leaf CO_2 assimilation rates cannot fully explain the effect on DW accumulation. They also suggested that the cause was Pn measurements at a single point, and diurnal Pn and dark respiration measurements of single leaves or whole canopies would be useful to determine the fate of carbon in plants grown under light of different qualities. The transpiration rate was higher under FL than G510. This result indicated that the uptake of nutrients in lettuce plants irradiated with G510 might be low. Therefore, leaf CO_2 accumulation rates under FL and G510 were similar, but nitrogen assimilation in the plants treated with FL and G510 might differ.

Since plants reflect green light, many researcher believed that lettuce plants would grow abnormally. However, lettuce plants grown under high-intensity (≥PPF 300) green LED light developed normally like plants grown under FL. This result indicated that green light at high intensity was available to the plant for morphogenesis and photosynthesis. The absorption of red or blue light by plant leaf pigments was about 90%, and that of green light was about 70–80% (Terashima et al., 2009). Therefore, the green light at PPF 100 might penetrate the leaf insufficiently for morphogenesis or photosynthesis, but might penetrate sufficiently at PPF 300.

In this study, the greatest effect of green LED light on plant growth was achieved with G510. The spectrum of green LED light includes long blue wavelengths (450–499 nm), and the proportion of long blue wavelengths emitted by G510 was the highest of the green LED lights used (Table 3). Folta and Maruhnich (2007) reported that plants have sensitive green-light sensors, namely phytochromes and cryptochromes, but their efficiency in processing green light is poor compared with their ability to respond to red and blue wavelengths. The transpiration rate of lettuce plants irradiated with G510 was higher than that of plants treated with the other green LEDs, and stomatal conductance with G510 was also higher than the other treatments (data not shown). It is hypothesized that the wavelengths emitted by G510 were also absorbed by phototropin, which is the blue-light receptor related to stomatal opening (Kinoshita et al., 2001). Stimulated phototropin is also important for vigorous plant growth (Takemiya et al., 2005).

In the green LED light treatments, G530 emitting high-intensity light (PPF 260) did not suppress succulent growth, whereas G510 and G520 at PPF >200 μmol m^{-2} s^{-1} suppressed succulent growth. Cryptochrome mediated the blue light inhibition of the hypocotyl elongation (Koornneef et al., 1998; Lin et al., 1998). The cryptochrome also absorbed the green light, so the green light might

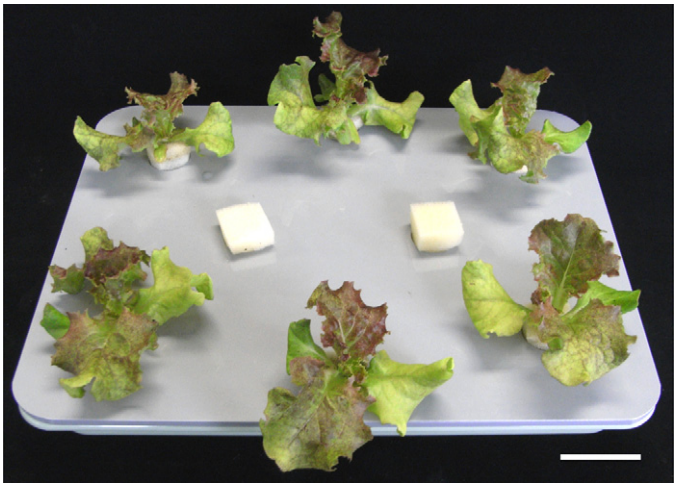

Fig. 5. Red leaf lettuce plants irradiated with the green light-emitting diode G510 (peak wavelength 510 nm) at PPF 500 μmol m^{-2} s^{-1} after 7 d irradiation. Bars indicate 5 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

also inhibit the hypocotyl elongation like the blue light. However, the total photon flux of green wavelengths (500–599 nm) in the G510 light emission at PPF 300 and that of G530 at PPF 260 were almost identical (254 and 260 μmol m^{-2} s^{-1}, respectively). Moreover, the ratio of short green wavelengths (500–549 nm) in the G510 light emission at PPF 300 and that of G530 at PPF 260 were also identical (84%), but G530 emitted 16% long green wavelengths (550–599 nm). These results indicated that lettuce plants recognized the composition of green light, and short-wavelength green light might be available for plant growth but long green wavelengths might not.

In conclusion, high-intensity green LED light was effective for stimulating plant growth and, in particular, short-wavelength of green light was available for active plant growth. The light emission of G510 had the greatest effect on plant growth in this study. The lettuce seedlings used in this study expressed anthocyanin in the leaves, and the expression in leaves irradiated with G510 at PPF 300 was lower than that of leaves irradiated with FL at PPF 100 (Fig. 2). However, irradiation with G510 at PPF >400 promoted anthocyanin expression in the leaf at a similar level to that with FL (Fig. 5). This result indicated that high intensity of green light stimulated the phenylpropanoid pathway in the lettuce plants. It will be interesting to study how green light drove the primary metabolism including the green light receptor and stimulated the secondary metabolism such as anthocyanin synthesis in the lettuce plant.

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