INTRODUCTION

The term “plant factory with artificial lighting” refers to a controlled environment that enables the production of pesticide-free plants with high yield and quality through the efficient use of water, nutrients, and labor within a small area (Merrill et al., 2016). Controlled conditions and inputs to create optimal conditions enable year-round production (Yamori et al., 2014). In many Asian, European, and North American countries, plant factories are used for commercial production of leafy greens, herbs, and seedlings (Hayashi, 2016). However, the technology is still being developed, and improvements are needed in construction and labor costs, electricity use, yield and quality, and the efficient use of light sources, e.g., fluorescent lamps and light-emitting diodes (LEDs) (Kozai, 2013). Currently, the production of leafy greens is managed with LEDs through the use of multiple culture shelves and an intensive cultivation pattern, but shading of outer leaves by the canopy reduces photosynthetic rate and accelerates the senescence of the outer leaves, which have to be trimmed before packaging and shipment, resulting in yield losses of over 10% (Zhang et al., 2015; Kozai and Niu, 2016).

Photosynthesis underlies plant growth and productivity (Yamori, 2016; Yamori and Shikanai, 2016). Light is one of the most important environmental factors that influence plant growth, and is not only the basic driving force of photosynthesis, but also an important regulator of plant growth and development (Terashima et al., 2006). Low light intensity restricts the photosynthetic rate, and if the light intensity falls below the compensation point (i.e., the PPFD at which photosynthetic rate is zero), carbon is lost. Low light also triggers leaf senescence, resulting in yield loss (Frantz et al., 2000). More than 90% of crop biomass is derived from photosynthetic products, so the enhancement of leaf photosynthesis should increase yield (Long et al., 2006; Yamori et al., 2011; 2016).

As well as light intensity, light quality greatly affects photosynthesis and plant growth (McCree, 1971; Inada, 1976, Lin et al., 2013). 80 to 95% of blue and red light is absorbed by chlorophyll in leaves across a broad range of plant species (Terashima et al., 2009; Muneer et al., 2014). Red light promotes photosynthesis and induces hypocotyl elongation and leaf area expansion; blue light regulates chlorophyll biosynthesis and suppresses cell elongation (McNeillis and Deng, 1995; Han et al., 2017). Leaf senescence can be suppressed by the application of red light in soybean (Giumet et al., 1989) and sunflower (Rousseaux et al., 1996), and of blue light in wheat (Causin et al., 1994).
2006). In contrast, green light is considered not to be efficient since it is absorbed weakly by chlorophyll (Sun et al., 1998). However, recent studies showed that green light might play an important role in photosynthesis (Terashima et al., 2009; Johkan et al., 2012), since it can penetrate the plant canopy better than blue or red light (Klein, 1992), and leaf photosynthesis and plant biomass are higher in plants grown under cool white fluorescent lamps, which emit light consisting of blue, green, and red wavelengths, than under red LED alone or red LED with blue light from fluorescent lamps (Yorio et al., 2001). Thus, the effect of different light wavelengths on plant growth and development is still unclear.

It has been proposed that supplemental upward lighting with LED from underneath plants could retard senescence in the outer leaves of leafy vegetables (Zhang et al., 2015). Moreover, a recent study analyzed the effect of supplemental upward lighting underneath the plants on photosynthetic characteristics and yield in comparison with supplemental downward lighting with white LEDs from above the plants at the same light intensity (taking account of the same electricity bill), and concluded that supplemental upward lighting efficiently reduced the wastage rate and resulted in increased yield compared with supplemental downward lighting at the same light intensity (Joshi et al., 2017). However, the most efficient wavelength for supplemental upward lighting has not been elucidated under the current leafy green production system. Therefore, we investigated the effect of supplemental upward lighting of different wavelengths (blue, green, red, and white) and intensity on the retardation of outer leaf senescence, photosynthesis, growth, and yield in romaine lettuce.

MATERIALS AND METHODS

Plant materials and growth conditions
Seeds of romaine lettuce (Lactuca sativa L. var. romana; Takii Seed Co., Kyoto, Japan) were sown in urethane cubes (W 2.3 cm×D 2.3 cm×H 2.7 cm). Seedlings were raised in an environment-controlled growth chamber under cool white fluorescent lamps at 350 μmol m⁻² s⁻¹ PPFD for 12 hours. At 28 days after sowing, uniform-sized seedlings at the five-leaf stage were transplanted in a growth room with a light/dark period of 14 hours and day/night air temperature of 25/20°C. All plants were grown in a deep-flow hydroponic system at a plant density of 33 plants m⁻² using Enshi formula nutrient solution (EC, 2.0±0.2; pH, 7.0±0.5; modified from Asao et al., 2013).

Supplemental upward lighting treatment
Cool white fluorescent lamps (Panasonic, FPR96EX-NA) with 200 μmol m⁻² s⁻¹ PPFD at plant level were used as the light source for downward lighting (plants grown solely under downward lighting as the control, Fig. 1). Four types of LED (blue, green, red, and white LEDs which is fabricated by a blue LED chip with yellow/red phosphors) provided supplemental upward lighting (PPFD of either 30 or 60 μmol m⁻² s⁻¹ at 3 cm above the light sources; Fig. 1) with the downward lighting. The LEDs were installed on aluminum plates to dissipate the heat and ensure that the leaf temperature was not significantly affected. The experiments were repeated twice independently, and each data point was the mean of three replicates (n = 6).

Leaf gas exchange measurements
The plants were divided into two layers of leaves, in which the 1st to 3rd leaves were considered the outer layer and the 4th to 6th were considered the inner layer. The photosynthetic rate of the outer (3rd) leaves in plants grown for 56 days after sowing was measured under each growth-light condition with a portable photosynthesis system (LI-6400XT; Li-Cor Inc., Lincoln, NE, USA) as described in Yamori et al. (2009, 2010). The portable photosynthesis system was fitted with a modified standard leaf chamber in which in addition to the top of the chamber, the bottom was equipped with a Propafilm window (6400-08 Clear Chamber Bottom). Since this clear chamber bottom transmits irradiation from beneath, it allows the analysis of the effect of supplemental upward lighting on the outer leaves.

Fig. 1 Schematic diagram of experiment and relative spectral photon flux of light sources used for supplemental upward lighting. (A) Diagrams show growing conditions under cool white fluorescent lamps (I) without (control) and (II) with supplemental upward lighting. Leaves were divided into outer layer (1st to 3rd leaves) and inner layer (4th to 6th leaves). (B) Wavelengths of cool white fluorescent lamps and white, blue, green, and red LEDs recorded at 240–800 nm with a spectroradiometer (SR9910-V7; Irradiant Ltd., Tranent, UK).
SUPPLEMENTAL UPWARD LIGHTING

The measurement chamber maintained a leaf temperature of 25°C, a CO₂ concentration of 400 μmol mol⁻¹, and a relative humidity of 60%.

We evaluated photosynthetic light-response curves in the 3rd leaves. Downward lighting was provided by a Li-6400-18A RGB light (0, 50, 100, 200, 300, 400, 600, or 800 μmol m⁻² s⁻¹ PPFD; Li-Cor Inc.; https://www.licor.com/documents/249cq0bchrypg21cvt1h) in the presence of the supplemental upward lighting. We used the response of photosynthetic rate to light to evaluate the curvature factor (θ) (Ögren and Evans, 1993).

Chlorophyll fluorescence analysis

Leaf discs (1.3 cm in diameter) taken from each leaf in plants grown for 64 days after sowing were placed abaxial surface up in 24-well plates filled with 1.5 mL 0.005% Triton-100, and gas was extracted from the discs at −0.1 MPa for 10 minutes in a vacuum chamber in order to prevent drying of leaf samples for preparations of 24 leaf discs. After 30 minutes in darkness, maximum photochemical efficiency of PSII (Fv/Fm) was measured by Imaging PAM (M-series; Heinz Walz GmbH, Effeltrich, Germany). Initial chlorophyll fluorescence (F₀) was measured under weak light (≤ 1 μmol m⁻² s⁻¹) at a low frequency (1 Hz). Maximum chlorophyll fluorescence (Fm) was assessed after illumination with saturating light (2700 μmol m⁻² s⁻¹) for 0.8 seconds. The variable fluorescence yield (Fv) was determined as Fm - F₀. The efficiency of excitation energy captured by open PSII reaction centers in dark-adapted leaf disc samples was estimated as Fv/Fm (Zhang et al., 2015).

Plant growth analysis

Lettuces were harvested at 66 days after sowing. Marketable leaf fresh weight, waste percentage, and total leaf fresh weight were measured. Marketable leaves were selected as leaves with more than 50% of chlorophyll content compared to the maximum values within a plant.

Determinations of leaf chlorophyll, ascorbic acid, and nitrate contents

The total chlorophyll content was determined by using N,N-dimethylformamide in the same leaf used for Fv/Fm measurements (Porra et al., 1989). The ascorbic acid and nitrate contents of outer and inner leaves were measured separately with an RQFlex Plus reflectometer (Merck, Darmstadt, Germany) as described in Zhang et al. (2015).

Statistical analysis

Analysis of variance (ANOVA) followed by Tukey’s test was conducted in SPSS statistical software (SPSS, Chicago, IL, USA). P < 0.05 was considered statistically significant.

RESULTS

Leaf characteristics

Without supplemental upward lighting, the total chlorophyll content (Fig. 2A, B, Fig. S1 and Table S1) and Fv/Fm values (Fig. 2C, D, Fig. S1 and Table S2) in control plants remained high in the 4th to 6th (inner) leaves, but decreased steeply from the 3rd to the 1st (outer) leaves.

With supplemental upward lighting, irrespective of wavelength, both PPDFs resulted in significantly higher total chlorophyll content and Fv/Fm values in the 1st and 2nd leaves than in control plants. Supplemental upward lighting with red LEDs gave the highest chlorophyll content and Fv/Fm values in the outer leaves (Table S1, S2).

Leaf gas exchange

Without supplemental upward lighting, the outer leaves of the control plants showed an obvious negative net photosynthetic rate (Fig. 3 and Fig. S2), since white fluorescent lamps from downward lighting did not reach to the outer leaves. With supplemental upward lighting, the net photosynthetic rate became positive; that at 60 μmol m⁻² s⁻¹ was nearly double (90% higher) than that at 30 μmol m⁻² s⁻¹ at each wavelength (Fig. 3). Among wavelengths, the net photosynthetic rate was highest with red and blue LEDs at 60 μmol m⁻² s⁻¹ (Fig. 3). The light-saturated photosynthetic rate at 800 μmol m⁻² s⁻¹ was similar under all light conditions (Fig. 4 and Table S3). The curvature factor (θ) of the photosynthetic light-response curve was increased significantly relative to the control by all treatments and tended to increase with light intensity (Table 1).

Plant growth

Supplemental upward lighting at all wavelengths greatly improved plant growth relative to the control (Fig. 2).
increased the content relative to those at 30 mleaves, achieving high marketable yields, especially at 60 red LEDs at 60 acid content in the outer leaves (Fig. 6A). White, blue, and gave the highest marketable weight (Fig. 5).

ing with red and blue LEDs reduced waste the most and ing upward lighting increased the ascorbic 2 s 1 PPFD without any supplemental upward lighting. “White 30”, “Blue 60”, etc. denote plants grown under downward lighting with supplemental white, blue, green, or red upward lighting at 30 or 60 mol m 2 s 1 PPFD. Data are means SEM (n = 5).

The photosynthetic rate was measured in the 3rd leaves of lettuce plants grown without or with supplemental upward LED lighting of 30 or 60 mol m 2 s 1 PPFD at 56 days after sowing. Values within a column followed by the same letter are not significantly different (Tukey’s HSD test, P < 0.05). “Control” denotes plants grown solely under downward lighting at a 200 mol m 2 s 1 PPFD without any supplemental upward lighting; “White 30”, “Blue 60”, etc. denote plants grown with supplemental white, blue, green, or red upward lighting at 30 or 60 mol m 2 s 1 PPFD. Data are means SEM (n = 5).

and red gave the highest value (Fig. 6A). No significant difference among treatments was observed in inner leaves (Fig. 6B). In all treatments, the nitrate content remained level of 450 mg 100 g below the European Commission maximum recommended difference among treatments was observed in inner leaves (Fig. 6B). In all treatments, the nitrate content remained level of 450 mg 100 g below the European Commission maximum recommended

5). It significantly reduced the waste of outer senescent leaves, achieving high marketable yields, especially at 60 mol m 2 s 1 PPFD (Fig. 5). Supplemental upward lighting with red and blue LEDs reduced waste the most and gave the highest marketable weight (Fig. 5).

Ascorbic acid content

Supplemental upward lighting increased the ascorbic acid content in the outer leaves (Fig. 6A). White, blue, and red LEDs at 60 mol m 2 s 1, but not green, significantly increased the content relative to those at 30 mol m 2 s 1, and red gave the highest value (Fig. 6A). No significant difference among treatments was observed in inner leaves (Fig. 6B). In all treatments, the nitrate content remained below the European Commission maximum recommended level of 450 mg 100 g FW (Fig. S3).

There was a strong positive correlation between marketable leaf fresh weight and ascorbic acid content (Fig. S4A), whereas strong negative correlation between waste and ascorbic acid content (Fig. S4B).

DISCUSSION

Shading of outer leaves by upper leaves and neighboring plants at high plant density in plant factories causes rapid senescence. These yellow leaves have to be trimmed, resulting in a loss of up to 10% of yield (Zhang et al., 2015; Kozai and Niu, 2016; Joshi et al., 2017). Supplemental upward lighting with white LEDs can retard outer leaf senescence and increase the photosynthetic rate, increasing the marketable yield (Joshi et al., 2017). We investigated the optimum wavelength and intensity of light to retard senescence and improve photosynthesis and thus yield. Our results clearly show that (1) supplemental upward lighting of any type of LEDs (blue, green, red, and white) retarded outer leaf senescence (Fig. 2 and Fig. S1), improved photosynthesis with increasing intensity at all wavelengths (Figs. 3, 4 and Fig. S2) and improved marketable leaf fresh weight (Fig. 5); (2) blue, red, and white LEDs increased ascorbic acid content (Fig. 6).

Supplemental upward lighting with red, blue, or white LED retards senescence and increases ascorbic acid content of outer leaves.

The degradation of chlorophyll is characteristic of leaf senescence (Richmond and Lang, 1957; Brouwer et al., 2012). Chlorophyll is essential for photosynthesis, and its content directly controls photosynthetic ability (Evans
Shading by the canopy reduced the chlorophyll content and $Fv/Fm$ values in outer leaves, but supplemental upward lighting maintained both (Fig. 2 and Fig. S1), thus retarding senescence. The retardation of senescence differed among wavelengths. Red, blue, green, and white (comprising blue, green, and red; Fig. 1) irradiation delayed senescence to the same degree (Fig. 2 and Fig. S1). In wheat, blue light retarded senescence through effects on oxidative metabolism (Causin et al., 2006). In postharvest broccoli, on the other hand, red light suppressed ethylene production, delaying senescence, better than blue light (Ma et al., 2014). Thus, both red and blue irradiation could retard senescence efficiently, albeit by different mechanisms.

It has been reported that the content of antioxidants, including ascorbic acid, is greatly affected by wavelength, especially red (Moss and Loomis, 1952; Zhou and Singh, 2002; Valpuesta and Botella, 2004; Wu et al., 2007; Bliznikas et al., 2012; Sirtautas et al., 2012; Deng et al., 2017) and blue (Ohashi-Kaneko et al., 2007; Li et al., 2012) light, 90% of which is absorbed by chlorophyll. Our data clearly show that blue, red, and white LEDs increased the ascorbic acid content of the outer leaves of romaine lettuce by 10% (Fig. 6) relative to conventional cultivation (Llorach et al., 2008; Zhan et al., 2013). In addition, in all treatments, the nitrate content remained below the European Commission maximum recommended level of 450 mg 100 g FW (Fig. S3; Alexander et al., 2008). We conclude that supplemental upward lighting with red, blue, or white LEDs is effective for both retarding leaf senescence and improving ascorbic acid content (Fig. S5). As white LEDs become more common for household lighting, the price is decreasing (Humphreys, 2008). Thus, white LEDs could be an ideal light source for commercial plant production in plant factories with artificial lighting, allowing high yields at low cost.

**CONFLICT OF INTEREST**

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**AUTHOR CONTRIBUTIONS**

WY conceived and designed the experiments. SS per-
formed the experiments. GZ, JJ and WY prepared the manuscript; and SS, JJ, GZ, MT, TK and WY contributed extensively to its finalization.

REFERENCES

Alexander, J., Benford, D., Cockburn, A., Cravedi, J.P., Dogliotti, E., Dake spec., A.D., Fernández-Cruz, M.I., Gremmels, J.F., Fürst,P., Gall,C., Grandjean,P., Gryl,J., Heinemeier,G., Johansson, N., Mutt,A., Schlatter, J., van Leeuwen, R., van Peteghem,C., Verger, P. 2008. Nitrate in vegetables scientific opinion of the panel on contaminants in the food chain. EFSA J 699: 1–79.

Asato, T., Asaduzzaman, M., Mondal, M. F., Tokura, M., Adachi, F., Ueno, M., Kawaguchi, M., Yano, S., Ban, T. 2013. Impact of reduced potassium nitrate concentrations in nutrient solution on the growth, yield and fruit quality of melon in hydroponics. Sci. Hort. 164: 221–231.

Bliznikas, Z., Zukauskas, A., Samuoliene, G., Virlé, A., Brazzyante, A., Jankauskiene, J., Duchovskis, P., Novikovas, A. 2012. Effect of supplementary pre-harvest LED lighting on the antioxidant and nutritional properties of green vegetables. Acta Hortic. 939: 85–91.

Brouwer, B., Zoiatkowska, A., Bagard, M., Keech, O., Garderström, P. 2012. The impact of light intensity on shade-induced leaf senescence. Plant Science 35: 1084–1098.

Causin, H. F., Jauregui, R. N., Barneix, A. J. 1998. The action spectrum, absorptance and leaf senescence in cowpea canopies. J. Am. Soc. Hort. Sci. 123: 694–701.

Guarnet, J. J., Willemoes, J. G., Montaldi, E. R. 1989. Modulation of progressive leaf senescence by the red : far-red ratio of incident light. Bot. Gaz. 150: 148–151.

Han, T., Vaganov, V., Cao, S., Li, Q., Ling, L., Cheng, X., Peng, L., Zhang, C., Yakovev, A. N., Zhong, Y., Tu, M. 2017. Improving “color rendering” of LED lighting for the growth of lettuce. Sci. Rep. 7: 1–7.

Hayashi, E. 2016. Current status of commercial plant factories with LED lighting market in Asia, Europe, and other regions. In: “LED Lighting for Urban Agriculture” (ed. by Kosai, T., Fujisawa, K., Runkle, E. S.), Springer, Singapore, p 295–308.

Humphreys, C. J. 2008. Solid-state lighting. MRS Bull. 33: 459–470.

Inada, K. 1976. Action spectra for photosynthesis in higher plants. Plant Cell Physiol. 17: 355–365.

Johkan, M., Shoji, K., Goto, F., Hahida, S. N., Yoshihara, T. 2012. Effect of green light wavelength and intensity on photomorphogenesis and photosynthesis in Lactuca sativa. Environ. Exp. Bot. 75: 128–133.

Joshi, J., Zhang, G., Shen, S., Supapulubutana, K., Watanabe, C. K. A., Yamori, W. 2017. A combination of downward lighting and supplemental upward lighting improves plant growth in a closed plant factory with artificial lighting. HortScience 52: 831–835.

Klein, R. M. 1992. Effects of green light on biological systems. Biol Rev Camb Philos Soc. 67: 199–284.

Kozai, T. 2013. Resource use efficiency of closed plant production system with artificial light: concept, estimation and application to plant factory. Proc. Jpn. Acad. Ser. B Phys. Biol. Sci. 89: 447–461.

Kozai, T., Niu, G. 2016. Plant factory as a resource-efficient closed plant production system. In “Plant Factory: An Indoor Vertical Farming System for Efficient Quality Food Production” (ed. by Kozai, T., Niu, G., Takagaki, M.), Elsevier, Amsterdam, p 69–90.

Li, H., Tang, C., Xu, Z., Liu, X., Han, X. 2012. Effects of different light sources on the growth of non-heading Chinese cabbage (Brassica campestris L.). J. Agric. Sci. 4: 262–273.

Lin, K. H., Huang, M. Y., Huang, W. D., Hsu, M. H., Yang, Z. W., Yang, C. M. 2013. The effects of red, blue, and white light-emitting diodes on the growth, development, and edible quality of hydropponically grown lettuce (Lactuca sativa L. var. capitata). Sci. Hortic. 150: 86–91.

Llorach, R., Martínez-Sánchez, A., Tomás-Barberán, F.A., Gil, M.I., Ferreres, F. 2008. Characterisation of polyphenols and antioxidant properties of five lettuce varieties and escarole. Food Chem. 108: 1028–1038.

Long, S. P., Zhu, X. G., Naidu, S. L., Ott, D. R. 2006. Can improvement in photosynthesis increase crop yields? Plant Cell Environ. 29: 315–330.

Ma, G., Zhang, L., Setiawan, C. K., Yamawaki, K., Asai, T., Nishikawa, F., Maezawa, S., Sato, H., Kanemitsu, N., Kato, M. 2014. Effect of red and blue LED light irradiation on ascorbate content and expression of genes related to ascorbate metabolism in postharvest broccoli. Postharvest Biol. Technol. 94: 97–103.

McCree, K. J. 1971. The action spectrum, absorbance and quantum yield of photosynthesis in crops plants. Agric. Meteor. 9: 191–216.

McNelis, T. W., Deng, X. W. 1995. Light control of seedling morphogenetic pattern. Plant Cell 7: 1749–1761.

Merrill, B. F., Lu, N., Yamaguchi, T., Takagaki, M., Maruo, T., Kozai, T., et al. 2016. The next revolution of agriculture: a review of innovations in plant factories. In “Handbook of Photosynthesis” (ed. by Pessarakli, M.), Ed 3. CRC Press, Boca Raton, FL, p 716–733.

Moss, R. A., Luomi, W. E. 1952. Absorption spectra of leaves. I. The visible spectrum. Plant Physiol. 27: 370–391.

Munere, S., Kim, E. J., Park, J. S., Lee, J. H. 2014. Influence of green, red and blue light emitting diodes on multiprotein complex proteins and photosynthetic activity under different light intensities in lettuce leaves (Lactuca sativa L.). Int J Mol Sci. 15: 4657–4670.

Oğren, E., Evans, J.R. 1993. Photosynthetic light-response curves I. The influence of CO2 partial pressure and leaf inversion. Planta 189: 182–190.

Ohashi-Kaneko, K., Takase, M., Noya, K. O. N., Fujiwara, K., Kurata, K. 2007. Effect of light quality on growth and vegetable quality in leaf lettuce, spinach and komatsuna. Environ. Control Biol. 45: 189–198.

Porra, R. J., Thompson, A. W., Kriedemann, P. E. 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochim. Biophys. Acta 975: 384–394.

Richmond, A. E., Lang, A. 1957. Effect of kinetin on protein content and survival of detached Xanthium leaves. Science 125: 650–651.
SUPPLEMENTAL UPWARD LIGHTING

Rousseaux, M. C., Hall, A. J., Sanchez, R. A. 1996. Far-red enrichment and photosynthetically active radiation level influence leaf senescence in field-grown sunflower. Physiol. Plant. 96: 217–224.

Sirtautas, R., Sakalauskienė, S., Jankauskienė, J., Duchovskis, P., Novickovas, A., Samusienė, G., Brazaitiūtė, A. 2012. The impact of supplementary short-term red LED lighting on the antioxidant properties of microgreens. In "Proceeding of the VII International Symposium on Light in Horticultural Systems 956". Acta Horticulturae, Cagliari, p 649–656.

Sun, J., Nishio, J. N., Vogelmann, T. C. 1998. Green light drives CO₂ fixation deep within leaves. Plant Cell Physiol. 39: 1020–1026.

Terashima, I., Hanba, Y. T., Tanoe, Y., Vyas, P., Yano, S. 2006. Irradiance and phenotype: comparative eco-development of sun and shade leaves in relation to photosynthetic CO₂ diffusion. J. Exp. Bot. 57: 343–354.

Terashima, I., Fujita, T., Inose, T., Chow, W. S., Oguchi, R. 2009. Green light drives leaf photosynthesis more efficiently than red light in strong white light: revisiting the enigmatic question of why leaves are green. Plant Cell Physiol. 50: 684–697.

Valpuesta, V., Botella, M. A. 2004. Biosynthesis of L-ascorbic acid in plants: new pathways for an old antioxidant. Trends Plant Sci. 9: 573–577.

Wu, M. C., Hou, C. Y., Jiang, C. M., Wang, Y. T., Wang, C. Y., Chen, H. H., Chang, H. M. 2007. A novel approach of LED light radiation improves the antioxidant activity of pea seedlings. Food Chem. 101: 1753–1758.

Yamori, W., Noguchi, K., Hikosaka, K., Terashima, I. 2009. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species. Plant Cell Physiol. 50: 203–215.

Yamori, W., Noguchi, K., Hikosaka, K., Terashima, I. 2010. Phenotypic plasticity in photosynthetic temperature acclimation among crop species with different cold tolerances. Plant Physiol. 152: 388–399.

Yamori, W., Takahashi, S., Makino, A., Price, G.D., Badger, M.R. von Caemmerer, S. 2011. The roles of ATP synthase and the cytochrome b₆/f complexes in limiting chloroplast electron transport and determining photosynthetic capacity. Plant Physiol. 155: 956–962.

Yamori, W., Zhang, G., Takagaki, M., Maruo, T. 2014. Feasibility study of rice growth in plant factories. J. Rice Res. 2: 1–6.

Yamori, W. 2016. Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress. J. Plant Res. 129: 379–395.

Yamori, W., Shikanai, T. 2016. Physiological functions of cyclic electron transport around photosystem I in sustaining photosynthesis and plant growth. Annu. Rev. Plant Biol. 67: 81–106.

Yamori, W., Kondo, E., Sugitani, D., Terashima, I., Suzuki, Y., Makino, A. 2016. Enhanced leaf photosynthesis as a target to increase grain yield: insights from transgenic rice lines with variable Rieske FeS protein content in the cytochrome b₆/f complex. Plant Cell Environ. 39: 80–87.

Yorio, N. C., Goins, G. D., Kagie, H. R., Wheeler, R. M., Sager, J. C. 2001. Improving spinach, radish, and lettuce growth under red light-emitting diodes (LEDs) with blue light supplementation. HortScience 36: 380–383.

Zhan, L., Hu, J., Ai, Z., Pang, L., Li, Y., Zhu, M. 2013. Light exposure during storage preserving soluble sugar and L-ascorbic acid content of minimally processed romaine lettuce (Lactuca sativa L. var. longifolia). Food Chem. 136: 273–278.

Zhang, G., Shen, S., Takagaki, M., Kozai, T., Yamori, W. 2015. Supplemental upward lighting from underneath to obtain higher marketable lettuce (Lactuca sativa) leaf fresh weight by retarding senescence of outer leaves. Front. Plant Sci. 6: 1–9.

Zhou, Y., Singh, B. R. 2002. Red light stimulates flowering and anthocyanin biosynthesis in American cranberry. Plant Growth Regul. 38: 165–171.