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Spectral Dependence of Electrical Energy-Based Photosynthetic Efficiency in A Single Leaf and Canopy under LED

LED 조명 하에서 단일엽과 군락의 스펙트럼에 대한 소비 전기 에너지 대비 광합성 효율 분석

BY

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COLLEGE OF AGRICULTURE AND LIFE SCIENCES
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SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF SEOUL NATIONAL UNIVERSITY

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ABSTRACT

In plant factories using LED as artificial light source, photosynthetic efficiency of crops and electrical energy consumption are affected by spectral characteristics of the LED. And most of previous observations on the spectral dependence of photosynthesis and optical property have been limited to a single leaf so far. The objectives of this study were to investigate photosynthetic efficiency and the related optical properties of four cultivars of lettuce (two reddish and two green leaves) and to quantify the spectral dependence of photosynthetic efficiency at the canopy level for selecting the optimum spectrum of LED regarding the electrical energy consumption. Absorptances, photosynthetic efficiencies of a single leaf of the plants, and electrical energy consumption of LED were measured at 18 wavelengths with a narrow band of 10 nm from 400 to 700 nm. Anthocyanin and chlorophyll contents (SPAD value) were measured to explain the difference between each cultivars. Light penetrations into crop canopy were estimated by models. Light absoprtances over PAR range were similar among the green and reddish lettuce cultivars, while that around 550 nm (green region) was slightly higher in the reddish leaves. Photosynthetic rates per incident photon of a single leaf had two peaks at 650-660 and 400-410 nm and those per absorbed photon (quantum yield) had three peaks at 650-660, 400-410, and 540-560 nm. In the green region of spectrum, both photosynthetic rates per incident photon and those per absorbed photon were lower in reddish cultivars than green ones. The differences in color and photosynthetic rate between reddish and green cultivars were due to anthocyanin contents in leaves. Spectral dependence of light absorptance at canopy level was much weaker than that at a single leaf. Light absorptance of green light was almost the same as that of blue or red light. As the quantum yield and absorptance of green light at canopy level was not lower than that of blue or red light, the photosynthetic efficiency of green light at canopy level became higher than that at the single leaf. Due to the fact that light conversion efficiency in terms of electrical energy consumption was lower in green LED than red or blue one, therefore, photosynthetic efficiency considering electrical energy consumption was much lower in green LED than that of blue or red LED even at canopy level. These results could reflect the actual plant response to light spectrum more accurately at canopy level and give more information to optimize the artificial lighting strategies for energy-saving.

Additional key words: lettuce, light conversion efficiency, light distribution, light penetration model, light property, light quality, plant factory

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INTRODUCTION

Artificial lightings have been often used in protected horticulture and plant factory because it could contribute to year-round production and product quality (Ieperen and Trouwborst, 2008; Heuvelink et al., 2006; Marcelis et al., 2006). Especially since LED has peculiar spectral properties (narrow-band spectrum) different from solar radiation, photosynthetic rate changes with a spectrum of LED even at the same intensity (Fujiwara, 2006; Morrow, 2008). In previous studies, it is known that most of plant crops reach two peaks at 650 nm in red region and at 450 nm in blue region (Balegh and Biddulph, 1970; McCree, 1972; Inada, 1976 and 1977; Evans, 1987) and this pattern is closely related with the absorption spectra of photosynthetic pigments (Atwell et al. 1999).

However, current knowledge about spectral dependence of photosynthesis has been limited so far to a single leaf level. In commercial practice of growth conditions, light sources are posited above the crop canopy and light distribution is not uniform along leaf layers. Paradiso *et al*. (2011) reported that at LAI = 3 and a light intensity of 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top of crop canopy, roughly 33% of the leaves in the lower and inner of the crop canopy received less than 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ due to self-shading. From an industrial point of view, it is more practical to consider optical properties of whole crop canopy than those of single leaf and estimate the photosynthetic efficiency at canopy level.

Unlike the greenhouse cultivation, plant factories using artificial lights have to pay for electrical energy consumption of lighting as a large proportion of total production expenses. Thus, maximization of both crop productivity and electrical energy efficiency is crucial in the plant factory using artificial lighting. To decide the optimal spectrum of LED, both spectral dependence of photosynthetic efficiency and light conversion efficiency of LED should be considered because the light conversion efficiency of LED varies with its emission spectrum.

The objectives of this study were to investigate the spectral dependence of photosynthetic rate and the leaf optical properties at a single leaf in 400-700 nm, to compare the photosynthetic rate between the single leaf and canopy level by using canopy transmittance model, and finally to decide the optimal spectrum of LED considering both efficient LED operation and crop photosynthesis at the canopy level.

LITERATURE REVIEW

Photosynthetic efficiency of plants

Photosynthetic efficiency of plant leaf is spectral-dependent (Hoover, 1937) because the absorption of incident irradiance by a leaf is dependent on wavelength due to the different absorptance spectra of the different leaf pigments (Inada, 1976) and also quantum yields efficiency of photons are dependent on the wavelength (McCree, 1972; Evans, 1987). Maximum quantum yields for C3 leaves were close to 0.093 mol CO_2 fixed (Long et al., 1993) or 0.106 mol O_2 evolved (Björkman and Demmig, 1987) per mol absorbed photons.

Three major causes for the wavelength-dependence of the quantum yield of absorbed photons have been categorized by Terashima (2009). First, photosynthetic carotenoids have different efficiency (35 to 90%) for excitation energy transfer to chlorophylls, depending on the type of carotenoid and its position within the photosynthetic apparatus, whereas the energy transfer efficiency in the antenna complexes from chlorophyll to chlorophyll is 100% (Hogewoning, 2012). Second, non-photosynthetic pigments, such as flavonoid and anthocyanin, which do not transfer any absorbed energy to the photosynthetic apparatus, absorb light in the blue and green region. Finally, the pigment composition and absorbance properties differ for photosystem I (PSI) and photosystem II (PSII); consequently, the balance of excitation between the two photosystems is wavelength-dependent (Evans, 1986, 1987; Chow et al., 1990; Melis, 1991; Walters and Horton, 1995). Any imbalance in excitation of the two photosystems results in quantum yield losses (Pfannschmidt, 2005).

Estimation of crop light interception

Various models were developed to calculate the crop light interception based on solar radiation. Lamber-Beer equation (Monsi and Saeki, 1953) was modified to quantitatively estimate the crop light interception.

$$I_{int} = 1 - \exp(-K_{crop} \cdot LAI) \tag{1}$$

Where, I_{int}, light intercepted into crop canopy, K_{crop}, light extinction coefficient of crop canopy and LAI, leaf area index ($m^2 \cdot m^{-2}$).

Goudriaan and Van Laar (1994) suggested equations to estimate crop light interception under the changes in ambient light environments and leaf optical properties such as proportion of diffuse light, ground reflectance and leaf scattering coefficients [eqns. (2)-(5)].

$$\sigma_{leaf} = \tau_{leaf} + \rho_{leaf} \tag{2}$$

$$K_{crop} = K_{bl}\sqrt{1 - \sigma_{leaf}} \tag{3}$$

$$\rho_{c,horiz} = \frac{1 - \sqrt{1 - \sigma_{leaf}}}{1 + \sqrt{1 - \sigma_{leaf}}} \tag{4}$$

$$\rho_c = \frac{2 \cdot K_{bl}}{K_{bl} + K_{bl,diff}} \cdot \rho_{c,horiz} \tag{5}$$

Where, τ_{leaf}, leaf transmittance; ρ_{leaf}, leaf reflectance; σ_{leaf}, leaf scattering coefficient; K_{bl}, the extinction coefficient of black leaf; $K_{bl,diff}$, K_{bl} for diffuse light; ρ_c, reflectance of crop canopy; $\rho_{c,horiz}$, ρ_c with horizontal leaf distribution.

LITERATURE CITED

Atwell, B., P. Kriedemann, and C. Turnbull, 1999. Plants in action – Adaptation in nature, performance in cultivation. Macmillan Education Australia Pty Ltd.

Balegh, S.E., and O. Biddulph, 1970. The photosynthetic action spectrum of the bean plant. Plant Physiol. 46**:**1–5.

Björkman, O., and B. Demmig, 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170:489–504.

Brazaityte, A., R. Ulinskaite, P. Duchovskis, G. Samuoliene, J.B. Siksnianiene, J. Jankauskiene, G. Sabajeviene, K. Baranauskis, G. Staniene, G. Tamulaitis, Z. Bliznikas, and A. Zukauskas, 2006. Optimization of lighting spectrum for photosynthetic system and productivity of lettuce by using light-emitting diodes LED. Acta Hort. 711:183–188.

Chow, W.S., A. Melis, and J. Anderson, 1990. Adjustments of photosystem stoichiometry in chloroplasts improve the quantum efficiency of photosynthesis. Proc. Natl. Acad. Sci. USA 87:7502–7506.

Evans, J.R., 1986. A quantitative analysis of light distribution between the two photosystems, considering variation in both the relative amounts of the chlorophyll-protein complexes and the spectral quality of light. Photobiochem. Photobiophys. 10:135–147.

Evans, J.R., 1987. The dependence of quantum yield on wavelength and growth irradiance. Aust. J. Plant Physiol. 14:69–79.

Farquhar, G.D., S. von Caemmerer, and J. Berry, 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149:78-90.

Fujiwara, K, and T. Sawada, 2006. Design and development of an LED-artificial sunlight source system prototype capable of controlling relative spectral power distribution. J. Light Visual Environ. 30:170-176.

Giusti, M.M., and R. Wrolstad, 2001. Characterization and measurement of anthocyanins by UV-visible spectroscopy. Curr. Protocols Food Anal. Chem. 2:1-13.

Goudriaan, J., and H. van Laar, 1993. Modelling potential crop growth processes. Current issues in production ecology (2) Kluwer Academic Publishers, Dordrecht, The Netherlands.

Heuvelink, E., M. Bakker, L. Hogendonk, J. Janse, R. Kaarsemaker, and R. Maaswinkel, 2006. Horticultural lighting in the Netherlands: new developments. Acta Hort. 711:25–34.

Hogewoning, S., 2010. On the photosynthetic and developmental responses of leaves to the spectral composition of light. Ph.D. thesis. Wageningen University.

Hogewoning, S., E. Wientjes, P. Douwstra, G. Trouwborst, W. van Ieperen, R. Croce, and J. Harbinson, 2012. Photosynthetic quantum yield dynamics: From photosystems to leaves. The Plant Cell 24:1921–1935.

Hoover, W., 1937. The dependence of carbon dioxide assimilation in a higher plant on wavelength of radiation. Smithsonian Ins. Misc. Collections 95:1–13.

Hopkins, W.G., 1999. Introduction to plant physiology, 2nd edn. John Wiley & Sons Inc.

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

Inada, K., 1977. Effects of leaf colour and the light quality applied to leaf-developing period on the photosynthetic response. Jpn. J. Crop Sci. 46:37–44.

Long, P., W. Postl, H. Bolharnordenkampf, 1993. Quantum yields for uptake of carbon dioxide in C3 vascular plants of contrasting habitats and taxonomic groupings. Planta 189:226–234.

Marcelis, L.F.M., A. Broekhuijsen, E. Meinen, E. Nijs, and M. Raaphorst, 2006. Quantification of the growth response to light quantity of greenhouse grown crops. Acta Hort. 711:97–104.

McCree, K.J., 1972. The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agric. Meteorol. 9:191–216.

Melis A., 1991. Dynamics of photosynthetic membrane composition and function. Biochim. Biophys. Acta 1058:87–106.

Monsi, M., and T. Saeki, 2005. On the factor light in plant communities and its importance for matter production. Ann. of Botany 95:549-567.

Morrow, R. C., 2008. LED lighting in horticulture. HortScience 43:1947-1950.

Paradiso, R, E. Meinen, J. Snel, P. Visser, W. van Ieperen, S. Hogewoning, and L. Marcelis, 2011. Spectral dependence of photosynthesis and light absorptance in sinlge leaves and canopy in rose. Sci. Hort. 127:548-554.

Pfannschmidt T., 2005. Acclimation to varying light qualities: Toward the functional relationship of state transitions and adjustment of photosystem stoichiometry. J. Phycol. 41:723–725.

Terashima, I., T. Fujita, T. Inoue, W. Chow, and R. Oguchi, 2009. Phototropins promote plant growth in response to blue light in low light environments. Plant Cell Physiol. 50:684–697.

van Ieperen, W., and G. Trouwborst, 2008. The application of LEDs as assimilation light source in greenhouse horticulture: a simulation study. Acta Hort. 810:1407-1414.

Walters, R.G., and P. Horton P., 1994. Acclimation of Arabidopsis thaliana to the light environment: Changes in composition of the photosynthetic apparatus. Planta 195:248–256.

MATERIALS & METHODS

Plant material and growth conditions

The experiment was carried out in plant factory modules in Seoul National University. Four leafy lettuce cultivars of ‘ChukMyeon’ and ‘ChiMa’ with reddish and green colours each were transplanted 20 days after seeding and grown during 20 days after transplanting (DAT). Day/night temperatures, relative humidity, and CO_2 concentration inside the plant factory were maintained at 22±1℃/16±1℃, 70±5%, and 1000±50 ppm, respectively. Light intensity at the crop level was set at a photon flux density of 145±10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ by LEDs with red:blue:white=8:1:1. Light period was 16h/8h at day/night. Nutrient solutions were composed according to Yamazaki’s solution for lettuce and maintained at EC 1.2 $dS \cdot m^{-1}$ and pH 6.5 in NFT system.

Plant growth and electrical energy consumption of LED

Leaf area and fresh weight were measured by a leaf area meter (LI-3100, LI-COR, Lincoln, USA) and a load cell (ADP-720L, Adam equipment, Danbury, USA) of lettuces at DAT 10 and DAT 20, respectively. Light conversion efficiency of each LED spectrum was measured by the electrical energy consumption to incident 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of PAR at 15 cm, using an electrical power meter (Inspetor Ⅱ SE, X4-LIFE, Braunschweig, Germany).

Photosynthetic rate at a single leaf

Photosynthetic rate on the top leaflet was measured by a CO_2/H_2O Gas analyser (LICOR 6400, LI-COR, Lincoln, NE, USA) connected to a IRGA leaf chamber (area: 6 cm^2). The conditions inside the IRGA chamber were kept constant as plant growth condition (temperature 22 ℃, CO_2 concentration 1000 ppm, relative humidity 70%, and air flow rate

204 μmol s^{-1}). Photosynthesis was measured at 18 wavelengths with a narrow band of 10 nm from 400 to 700 nm: 400-410, 420-430, 450-460, 460-470, 470-480nm in blue region, 490-500, 510-520, 520-530, 530-540, 540-55, 570-580, 580-590, 590-600nm in green region, and 610-620, 620-630, 630-640, 650-660, 690-700nm in red region. The LED provided a continuous band background light (150 μmol m^{-2} s^{-1}) on the leaf surface. Photosynthetic rate was calculated as μmol of CO_2 assimilated per μmol of incident light (150 μmol m^{-2} s^{-1}). Quantum yield was calculated as μmol CO_2 per μmol of absorbed light (150 μmol m^{-2} s^{-1}*absorptance).

Optical properties of leaf

Leaf transmittance (Tr) and reflectance (Ref) spectra of the top leaflet were measured between 300 and 110 nm (by bandwidth 1 nm) by a spectro-radoameter with an integrating sphere (LI-1800 spectro-radiometer, LI-COR, Lincoln, NE, USA) via fiber optic probe. Total Tr values were obtained through dividing light intensity transmitted through the leaf to that reflected one from the reference material. For transmission (or reflection) measurement, the leaf was clamped to the input port (or the exit port) of the integrating sphere with the bottom - abaxial side (or top - adaxial side) facing the integrating sphere. Leaf absorptance (Abs) was calculated as Abs = 100 – (Ref + Tr).

Anthocyanin and chlorophyll contents

Anthocyanin contents per fresh weight (μg･g^{-1}-FW) of four lettuces were measured by pH differential method (Giusti and Wrolstad, 2001). Chlorophyll contents were measured by a SPAD meter (SPAD-502, Minolta, Osaka, Japan) by means of 10 point per each leaf.

Canopy transmittance model

Crop light interception was estimated by using a modified Lamber-Beer equation (Monsi and Saeki, 1953).

$$I_{int} = 1 - \exp(-K_{crop} \cdot LAI) \tag{1}$$

where I_{int}, light intercepted into canopy, K_{crop}, light extinction coefficient of crop canopy, and LAI, leaf area index ($m^2 \cdot m^{-2}$).

Crop light interception according to changes in the ambient light environments and leaf optical properties such as proportion of diffuse light, ground reflectance and leaf scattering coefficient were estimated according to Goudriaan and Van Laar (1994) [eq. (2)-(5)].

$$\sigma_{leaf} = Tr_{leaf} + Ref_{leaf} \tag{2}$$

$$K_{crop} = K_{bl}\sqrt{1 - \sigma_{leaf}} \tag{3}$$

$$\rho_{c,horiz} = \frac{1 - \sqrt{1 - \sigma_{leaf}}}{1 + \sqrt{1 - \sigma_{leaf}}} \tag{4}$$

$$\rho_c = \frac{2 \cdot K_{bl}}{K_{bl} + K_{bl,diff}} \cdot \rho_{c,horiz} \tag{5}$$

where Tr_{leaf}, leaf transmittance; Ref_{leaf}, leaf reflectance; σ_{leaf}, leaf scattering coefficient; K_{bl}, extinction coefficient of black leaf; $K_{bl,diff}$, K_{bl} for diffuse light; ρ_c, reflectance of crop canopy; and $\rho_{c,horiz}$, ρ_c with horizontal leaf distribution.

Extinction coefficient, K_{bl} is for a crop with spherical leaf angle distribution and the value is known as 0.84 by previous studies (Paradiso, 2011)). In this study, reflection was subtracted from the incoming diffuse light. By the pattern that leaf scattering coefficient (σ_{leaf}) has different values with spectrum, the spectral dependence of light absorptance was calculated at crop canopy level.

Photosynthetic rate at crop canopy level

Photosynthetic rate at crop canopy level was calculated with spectral dependence of quantum yield at a single leaf and spectral dependence of light absorptance at crop canopy level.

RESULTS AND DISCUSSION

Light absorptance of lettuce culivars

The contents of anthocyanin in leaf tissues of ChukMyeon lettuce were higher in reddish leaves (219.04 ± 16.22 μ*g-FW^{-1}) than in green leaves (23 ± 10 μ*g-FW^{-1}) and of ChiMa lettuce was also higher in reddish leaves (209.40 ± 17.21 μ*g-FW^{-1}) than those in green leaves (45.04 ± 7.67 μ*g-FW^{-1}, n = 4; average ± SE). However, the contents of chlorophylls (SPAD value) in leaf did not show significant differences (Fig. 1). Lettuce leaves showed a high absorptance from 400 to 500 nm and from 650 to 680 nm, while showed a relatively value from 500 to 580 nm and drastic decrease above 700 nm (Fig. 2). In the whole PAR region (400-700 nm), the reddish leaves had a higher absorptance than green leaves in both lettuce cultivars. However, in blue (400-500 nm) and red (600-700 nm) regions, the reddish leaves and green leaves had similar absorptances. The gap of the absorptance in the PAR region by leaf color was due to different absorptance in green (500-600 nm) region (Table 1).

Spectral dependence of light absorptance measured in the leaves of four lettuce cultivars were similar to those reported by previous studies on various crop cultivars. In particular, both different lettuce cultivars absorbed more than 90% of the incident light in blue and red regions, similarly to those reported for strawberry (Inada, 1976), rice and perilla (Inada, 1977) grown in greenhouse, and for bean in growth chamber (Balegh and Biddulph, 1970). The spectral dependence of absorptance of leaf was also affected by pigment composition (Inada, 1980). Chlorophylls are a type of pigments known as contributing mostly to photosynthesis and have a high light absortptance in red and blue light (Gates et al., 1965). Carotenoids, which are less efficient (70%) in excitation energy transfer than chlorophylls has absortpance peak at lower spectrum than chlorophylls (Merzlyak, 1996; Terashima et al., 2009). Among the pigments not contributing to photosynthesis, flavonoid and anthocyanin absorb the lights in UV region (Havaux and Kloppstech, 2001) and green region (Merzlyak et al., 2008), respectively. In this study, light absorptance of lettuce leaves was very small under green light (500-600 nm) because of higher transmittance and reflectance in this region. The reddish leaves contained a higher concentration of anthocyanin and showed a higher absorptance of green light than green leaves. Similar results have been observed in several crops (Burger and Edwards, 1996; Woodall et al., 1998; Neill and Gould, 1999), indicating that the differences in absorptance of green light were attributed to the contribution of anthocyanin (Gould et al., 1995; Smillie and Hetherington, 1999).

Photosynthetic rate at a single leaf

Regardless of leaf colours of lettuce cultivars having reddish and green leaves, the photosynthetic rates reached the highest under blue light with one major peak at 400-410 nm and another higher peak in the red region (650-660 nm) (Fig. 3). A broad minimum was observed in the green region (500-600 nm) while drastic decrease above 650 nm with very low photosynthetic rate at 700 nm. In the whole PAR region, photosynthetic rate of green leaves was relatively higher than reddish leaves except for 450-460 nm of ChukMyeon lettuce, and 400-430and 610-660 nm of ChiMa lettuce (Fig. 3). These characteristics of higher photosynthetic rate in green leaves were clearly observed in the green region (Table. 2).

In this study, spectral dependence of photosynthetic rate at a single leaf was higher under red and blue lights like as that of light absortance of chlorophyll. Previous reports showed the similar pattern for a number of species (Inada, 1977, Burger; Edwards, 1996).

More precisely, photosynthetic rates of most crops had peaks at 650or 680 nm in red region and at 450 nm in blue region, and this light spectrum coincided to the chlorophyll spectral absorptance pattern (Hogewoning, 2010). However, in this study, photosynthetic rate of the lettuce cultivars had their peaks around 400-410 nm in blue region due to own characteristic of lettuce having its absorptance peak at UV region below PAR (Maas and Dunlap, 1989). Although lettuce leaves has similar chlorophyll contents regardless of leaf colour, spectral photosynthetic rate was dependent on light spectrum by leaf colour. Previous reports also showed similar patterns for various species; purple and reddish leaves had a higher absorptance but lower photosynthesis efficiency than green leaves under green wavelengths (Inada, 1977; Burger and Edwards, 1996; Dodd et al., 1998; Gould et al., 2002). This result was due to the content of anthocyanin. Particularly, it is known that these pigments in the cell vacuole can modify the photosynthetic performance by restricting the absorptance of green light by chlorophyll (Paradiso, 2011). It would function as “light filter”, reducing the quantum yield efficiency absorbed by chlorophyll (Gould et al., 2000).

The spectral quantum yield of photosynthesis (=fixed CO_2 by absorbed photons) was calculated with the spectral light absorptance (=absorbed photons / incident photons) and the spectral photosynthetic rate (=fixed CO_2 by incident photon). The spectral quantum yield reached the highest value in the 650-660 nm and 400-410 nm, for both the colour of leaves (Fig. 4). In red leaves, the quantum yield around 530-560 nm was almost the same as that at 650-660 nm for both lettuce cultivars. Unlike the photosynthetic rate, quantum yield in green region increased like in red or green region. This increase was more distinctly observed in green leaves than red leaves (Table. 3).

Photosynthetic rate at canopy level

At the single leaf, photosynthetic rate under green light was lower than blue or red light due to its low absorption by the leaves of four lettuce cultivars. However, a light absorptance model at crop canopy level showed that a large part of the transmitted and reflected green lights was absorbed by leaves at middle and low layers in the crop canopy, indicating that the absorption of green light was not much lower than that of red light (Fig. 5). For reddish leaves, the light absorptance of green light (500-600 nm) was 92.48% in ChukMyeon lettuce and that of red light (680 nm) was 93.63% in ChiMa lettuce at the leaf level, while 97.02% in ChukMyeon lettuce and 97.49% in ChiMa lettuce at the crop level. That is, the light absorptance of green light at canopy level was higher by 4% than that at a single leaf (Table 4). For green leaves, light absorptance at crop level was much greater than at the single leaf. The light absorptance of green light (500-600 nm) was 78.12% in ChukMyeon lettuce) and that of red light (680 nm) was 78.47% in ChiMa lettuce at the single leaf, while 90.50% in ChukMyeon lettuce and 90.71% in ChiMa lettuce at the crop level. The light absorptance of green light at canopy level was higher by 11% than that at a single leaf (Table 4.)

Light absorptance at crop canopy level, calculated by the models, has weaker spectral dependence than that at a single leaf. This fact means that the green light, reflected or transmitted on the upper leaves of canopy, gives more opportunity to reach the inner or lower leaves of the canopy. In this study, green cultivars had a weaker spectral dependence than reddish ones (Fig. 5). As the reddish cultivars absorbed more green lights at upper leaves of the canopy than the green cultivars, the penetration of the green light into the inner or lower leaves of the canopy was reduced.

For reddish leaves, the photosynthetic rate of green light (500-600 nm) was 58.32% in ChukMyeon lettuce and that of red light (650 nm) was 52.23% in ChiMa lettuceat the single leaf level, while 70.54% in ChukMyeon lettuce and 68.96% in ChiMa lettuce at the crop level. For green leaves, photosynthetic rate at the crop level was much greater than at the single leaf . The photosynthetic rate of green light (500–600 nm) was 69.04% in ChukMyeon lettuce and that of red light (650 nm) was 64.48% in ChiMa lettuce at the single leaf, while 96.60% in ChukMyeon lettuce and 98.57% in ChiMa lettuce at the crop level (Table. 5, Fig. 6). The light absorptance of green light at canopy level was higher by 22.65% than that at a single leaf. The calculated results showed an increased utilization of green light at canopy level rather than the single leaf, as indicated by photosynthetic efficiency. The reason of this result can be divided into two. First, the lower photosynthetic rate of green light is due to lower absorptance of green light. If the same photons were absorbed by leaves, the quantum yield of green light is not lower than that of red or blue light. Second, light absorptance at crop canopy level has a weaker spectral dependence than at a single leaf. In fact, green light was absorbed more at the canopy level than the single leaf.

Photosynthetic efficiency of LED based on electrical energy

Electrical consumption energy to incident the same light intensity of each spectrum was lower at blue (400-410 nm) and red (600-680 nm) LEDs. As green LED had a low light conversion efficiency, a lot of electrical energy was consumed for maintaining incident 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 7). Spectral dependence of LED light conversion efficiency was required by economic analysis of LED plant factory. Red or blue LED, having high industrial demands, was more efficient than green LED.

A photosynthetic efficiency for electrical energy had a peak at 450-460 nm (blue LED), 610-620, 620-630, and 650-660 nm (red LED). However, green LED, having low light conversion efficiency, showed a low photosynthetic efficiency for electrical energy (Fig.8). In red region, the photosynthetic efficiency was higher except for 630-640 nm LED, especially, 650-660 nm LED having high photosynthetic rate at canopy level and light conversion efficiency, was the most efficient. In blue region, 450-460 nm LED had the higher photosynthetic efficiency than 400-410 nm LED, which had highest photosynthetic rate but lower light conversion efficiency. Therefore, although green LED showed a high photosynthetic rate at the crop canopy level, the photosynthetic efficiency considering electrical energy consumption was lower than red or blue LED due to its lowlight conversion efficiency.

Table 1. Light absorptances by green and reddish leaves of lettuce cultivars at the wave lengths of visible, blue, green, and red regions.

Cultivars		PAR (400-700 nm)	Blue region (400-500 nm)	Green region (500-600 nm)	Red region (600-700 nm)
ChukMyeon	Reddish leaf	0.865b[z]	0.928a	0.831c	0.830c
	Green leaf	0.829c	0.926a	0.707d	0.841c
ChiMa	Reddish leaf	0.873b	0.930a	0.831c	0.830c
	Green leaf	0.829c	0.930a	0.707d	0.845c

[z] Mean separation by Duncan’s multiple range test at $P = 0.05$.

Table 2. Differences between photosynthetic rates of reddish and green lettuces with wavelength.

	Wave length (nm)	ChukMyeon	ChiMa
Blue region	400-430	0.340[z]	-0.134
	430-470	-0.299	0.323
	470-500	0.222	0.633
Green region	500-530	0.477 *	0.986 *
	530-570	0.497 *	0.702 ***
	570-600	0.392	1.007 ***
Red region	600-630	0.353	-0.209
	630-660	0.508	-1.045
	660-700	0.012	0.012

*, **, *** Significant at $P < 0.05$, 0.01 or 0.001 by Duncan's multiple range test, respectively.

[z] photosynthetic rate of green leaves – photosynthetic rate of reddish leaves

Table 3. Photosynthetic rates and Quantum yields of four lettuce cultivars in blue (400-500 nm), green (500-600 nm) and red (600-680 nm) regions.

	Photosynthetic rate (μmol·m^{-2}·s^{-1})				Quantum yield (μmol·μmol^{-1})			
	ChukMyeon		ChiMa		ChukMyeon		ChiMa	
	Reddish	Green	Reddish	Green	Reddish	Green	Reddish	Green
Blue region	6.046a^{z}	6.218a	6.299a	6.252a	0.043ab	0.044a	0.043b	0.045a
Green region	4.728b	5.174b	4.163b	5.074b	0.038b	0.048a	0.039b	0.047a
Red region	6.051a	6.481a	6.044a	5.929a	0.049a	0.051a	0.049a	0.045a

^{z}Mean separation within columns by Duncan's multiple range test at *P =0.05*.

Table 4. Light absorptances of four lettuce cultivars in 680 nm (Abs 680) and green region (Abs green) and percentage values of Abs green/Abs 680 (ratio) at a single leaf vs crop canopy level.

		Single leaf			Crop canopy level		
		Abs 680	Abs green	Ratio (%)	Abs 680	Abs green	Ratio (%)
ChukMyeon	Reddish leaves	0.896a[z]	0.829c	92.48	0.883a	0.857b	97.02
	Green leaves	0.912a	0.713c	78.12	0.889a	0.805b	90.50
ChiMa	Reddish leaves	0.898a	0.841c	93.63	0.883a	0.862b	97.49
	Green leaves	0.917a	0.720c	78.47	0.891a	0.808b	90.71

[z] Mean separation within columns by Duncan's multiple range test at $P = 0.05$.

Table 5. Photosynthetic rates of four lettuce cultivars in 650 nm (Pn 650), in green region (Pn green) and percentage values of Pn green/Pn 650 (ratio) at a single leaf vs crop canopy level.

		Single leaf			Crop canopy level		
		Pn 650	Pn green	Ratio (%)	Pn 650	Pn green	Ratio (%)
ChukMyeon lettuce	Reddish leaves	8.213a	4.789c	58.32	7.847a	5.536b	70.54
	Green leaves	7.657a	5.286c	69.04	7.093b	6.852b	96.60
ChiMa lettuce	Reddish leaves	8.177a	4.272c	52.23	7.35a	5.069b	68.96
	Green leaves	7.980a	5.145c	64.48	6.710b	6.610b	98.51

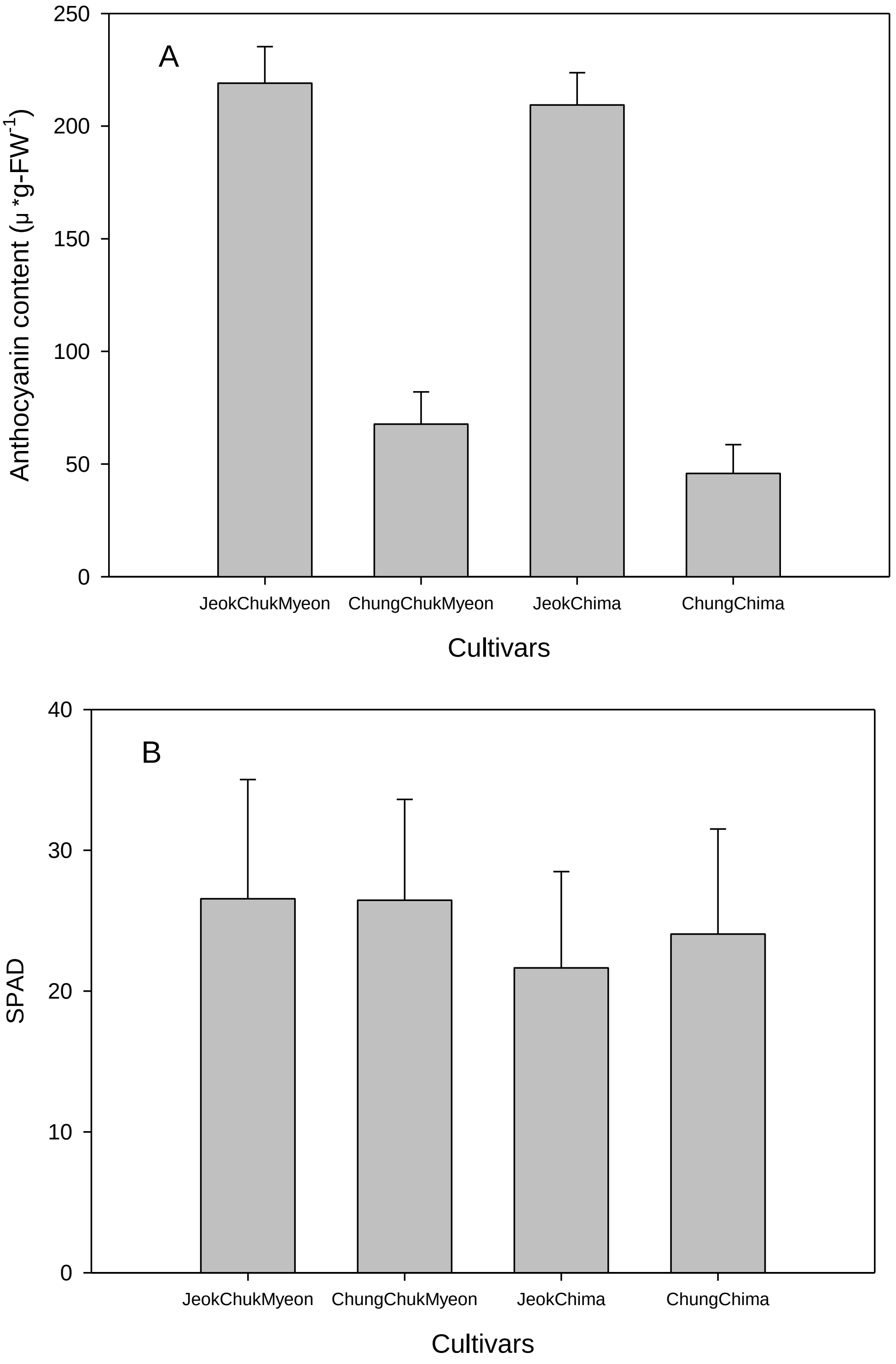


Fig. 1. Anthocyanin contents (A) and SPAD values (B) in leaf tissues of four lettuce cultivars.

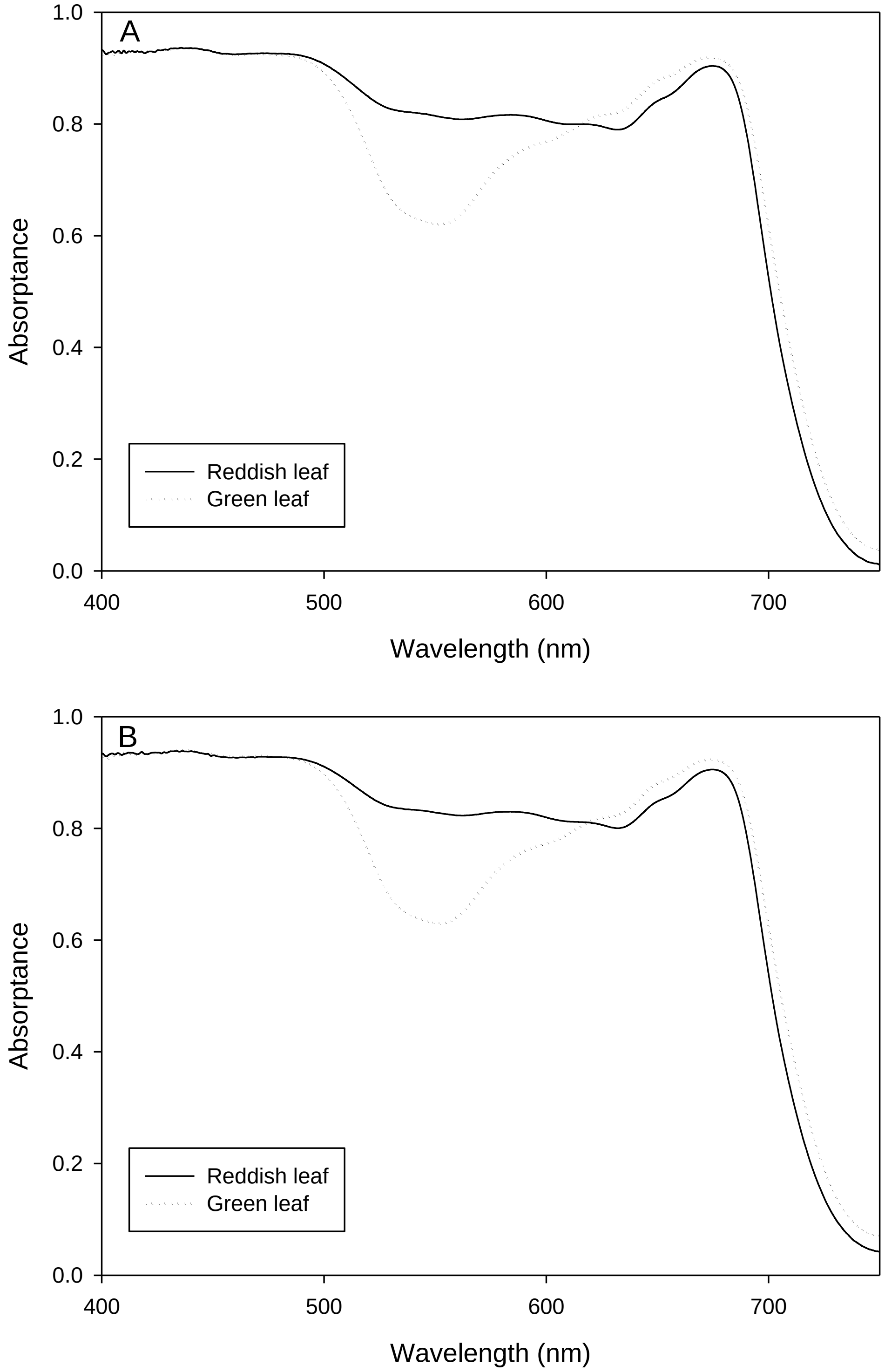


Fig. 2. Absorptance of spectra in green and reddish leaves of ChukMyeon (A) and ChiMa (B) lettuce cultivars.

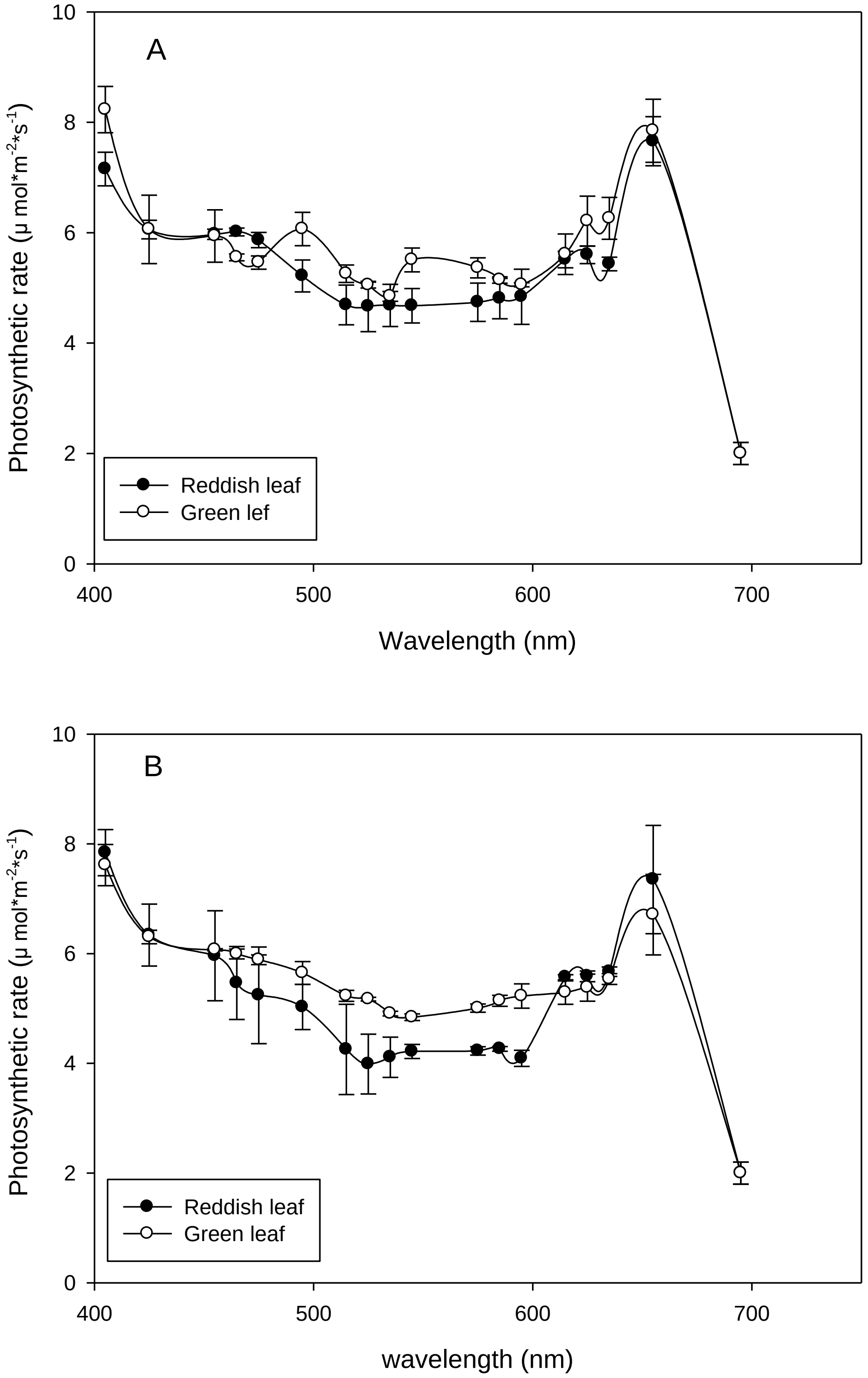


Fig. 3. Photosynthetic rates of reddish and green leaves of ChukMyeon (A) and ChiMa (B) lettuce cultivars.

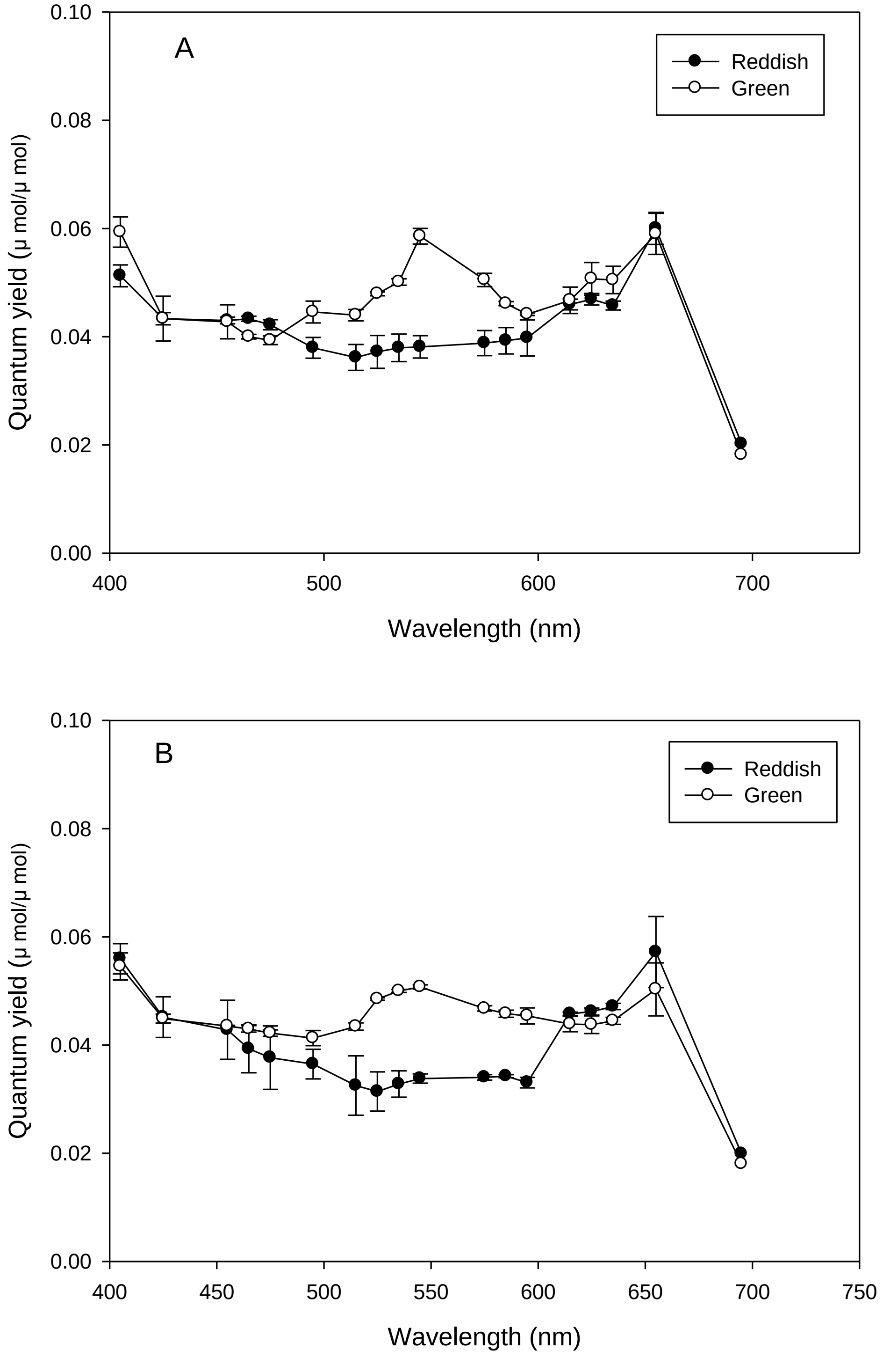


Fig. 4. Quantum yields of green and reddish leaves of ChukMyeon (A) and ChiMa (B) cultivars.

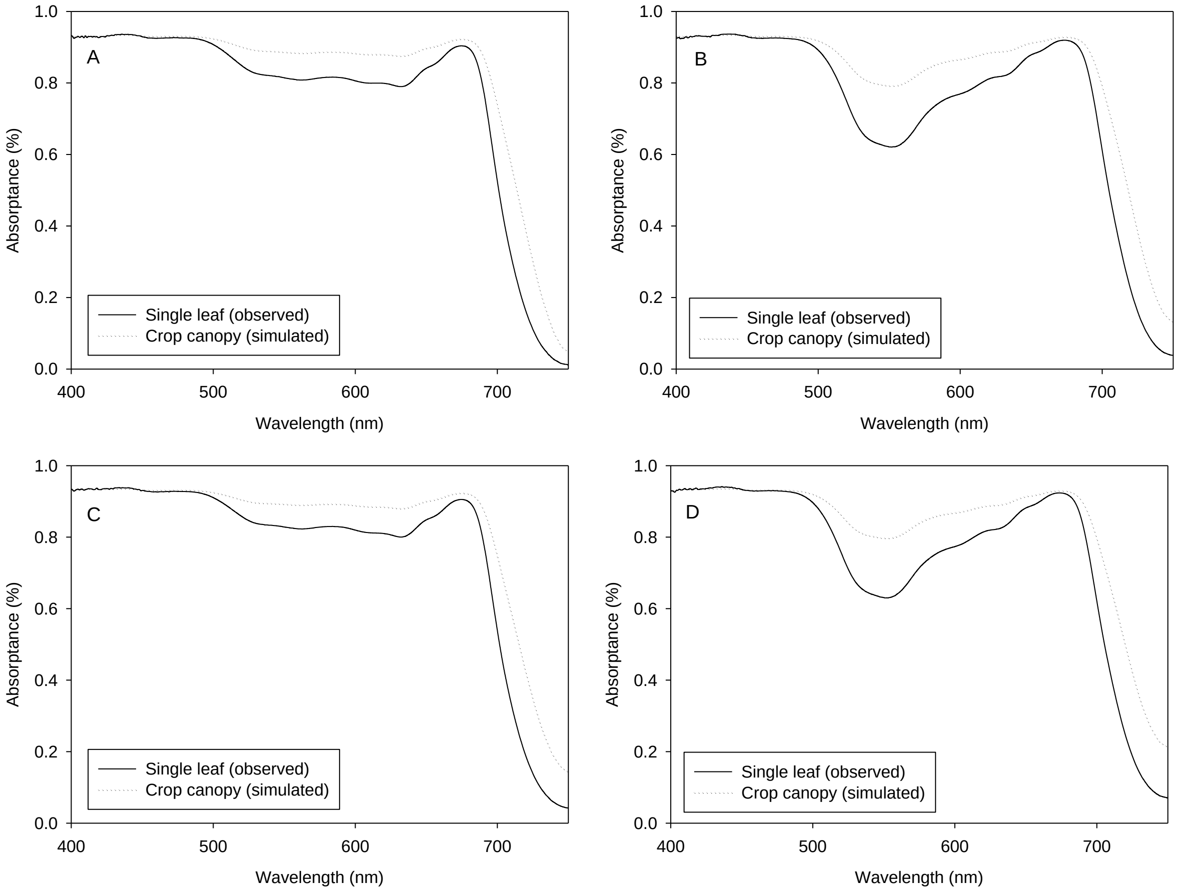


Fig. 5. Fraction absorptances simulated at crop level and observed at a single leaf for four lettuce cultivars. A, B, C, and D are JeokChukMyeon, ChungChukMyeon, JeoChiMa, and ChungChiMa, respectively.

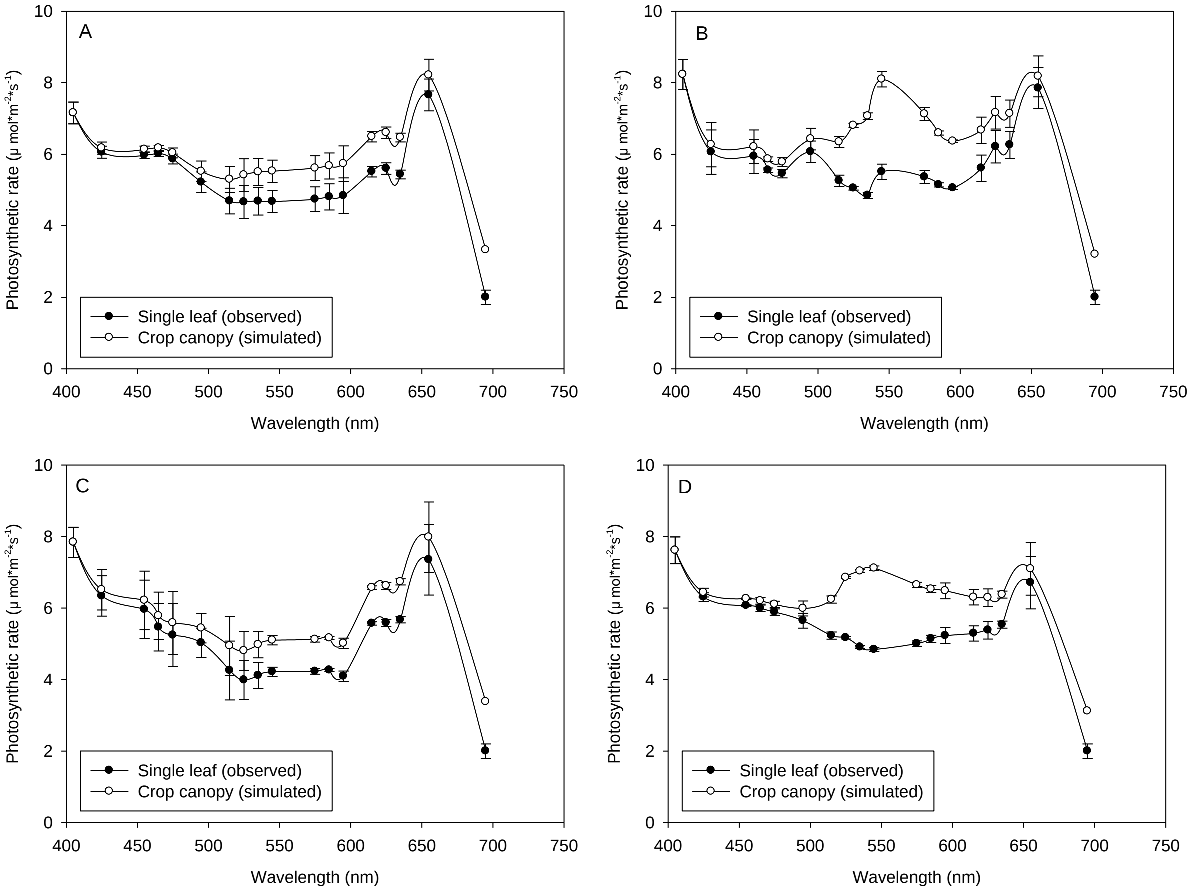


Fig. 6. Photosynthetic rate simulated at crop level and observed at a single leaf for four lettuce cultivars. A, B, C, and D are JeokChukMyeon, ChungChukMyeon, JeokChiMa, and ChungChiMa, respectively.

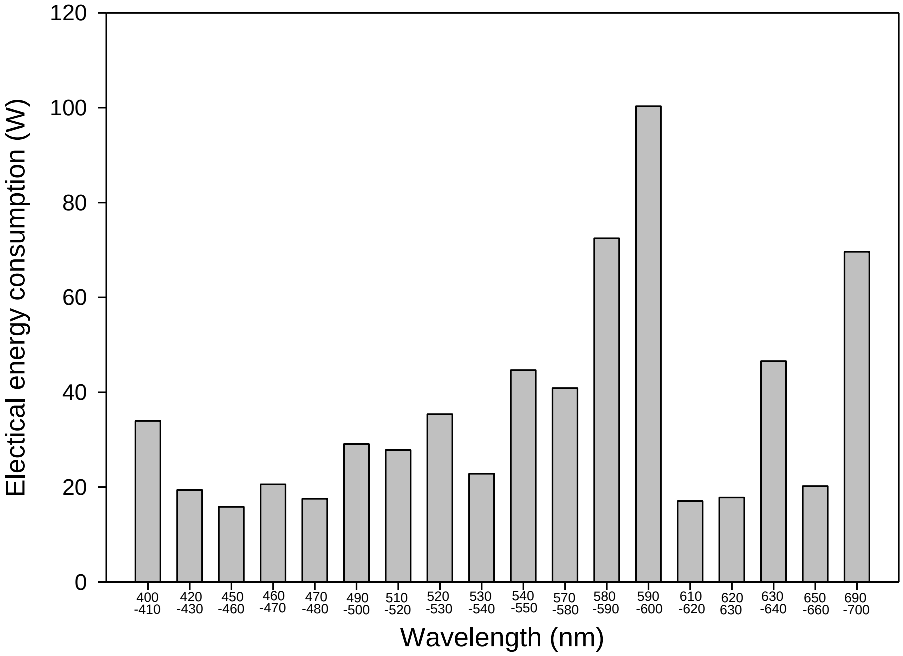


Fig. 7. Electrical energy consumption with wavelength of LED.

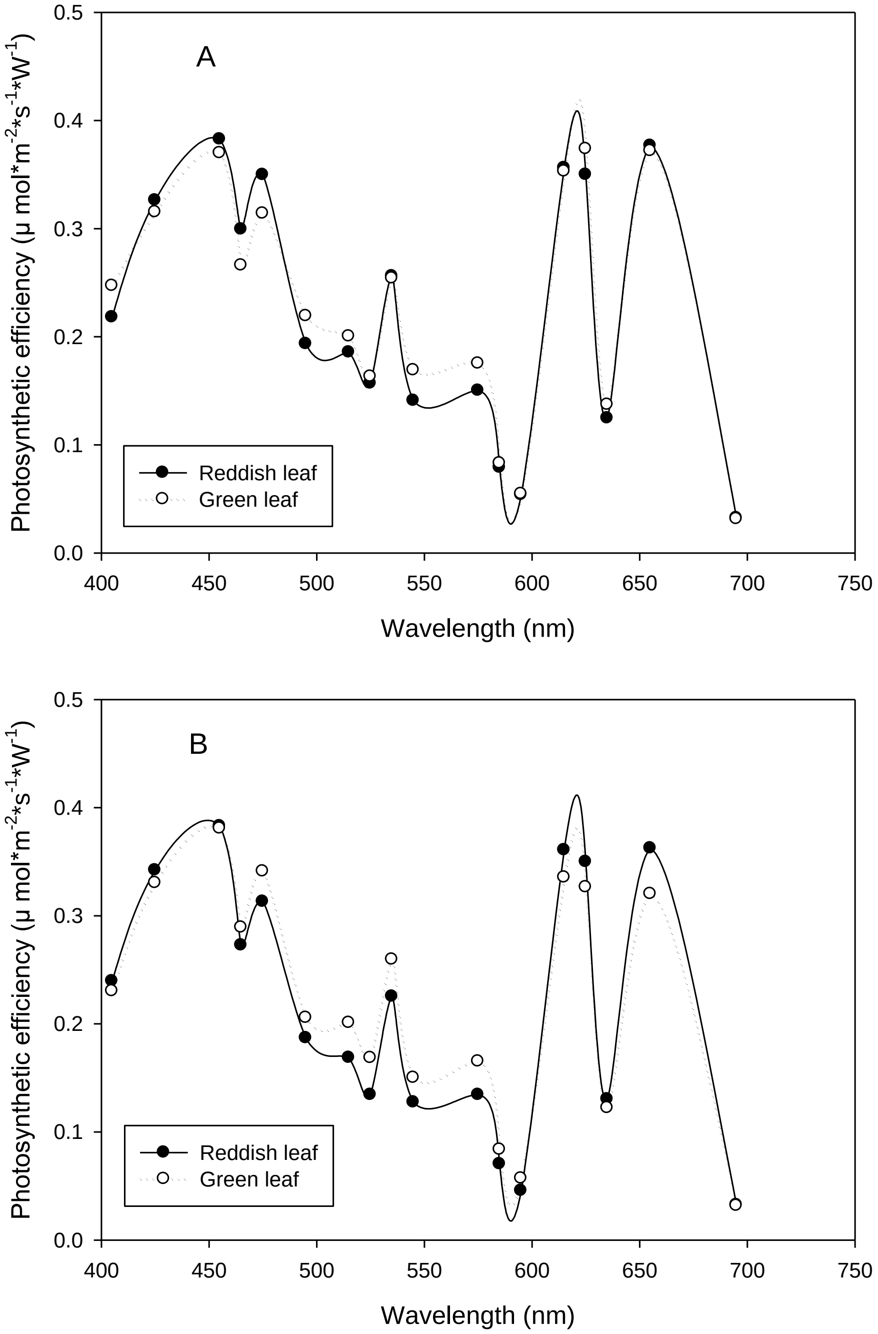
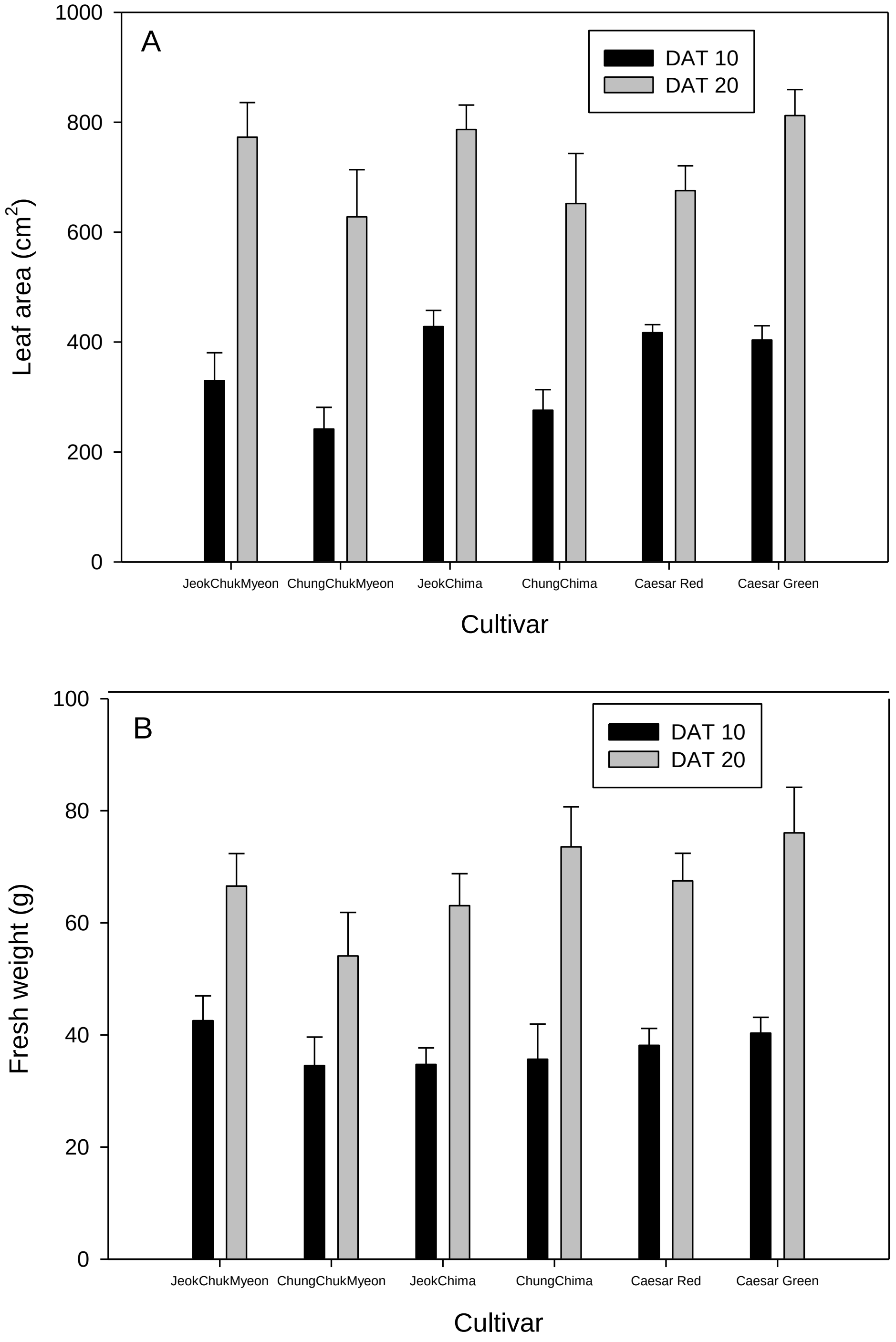


Fig. 8. Photosynthetic efficiencies for electrical energy (= Photosynthetic rates simulated at crop level / Electrical energy consumption) of ChukMyeon (A) and ChiMa (B) cultivars.

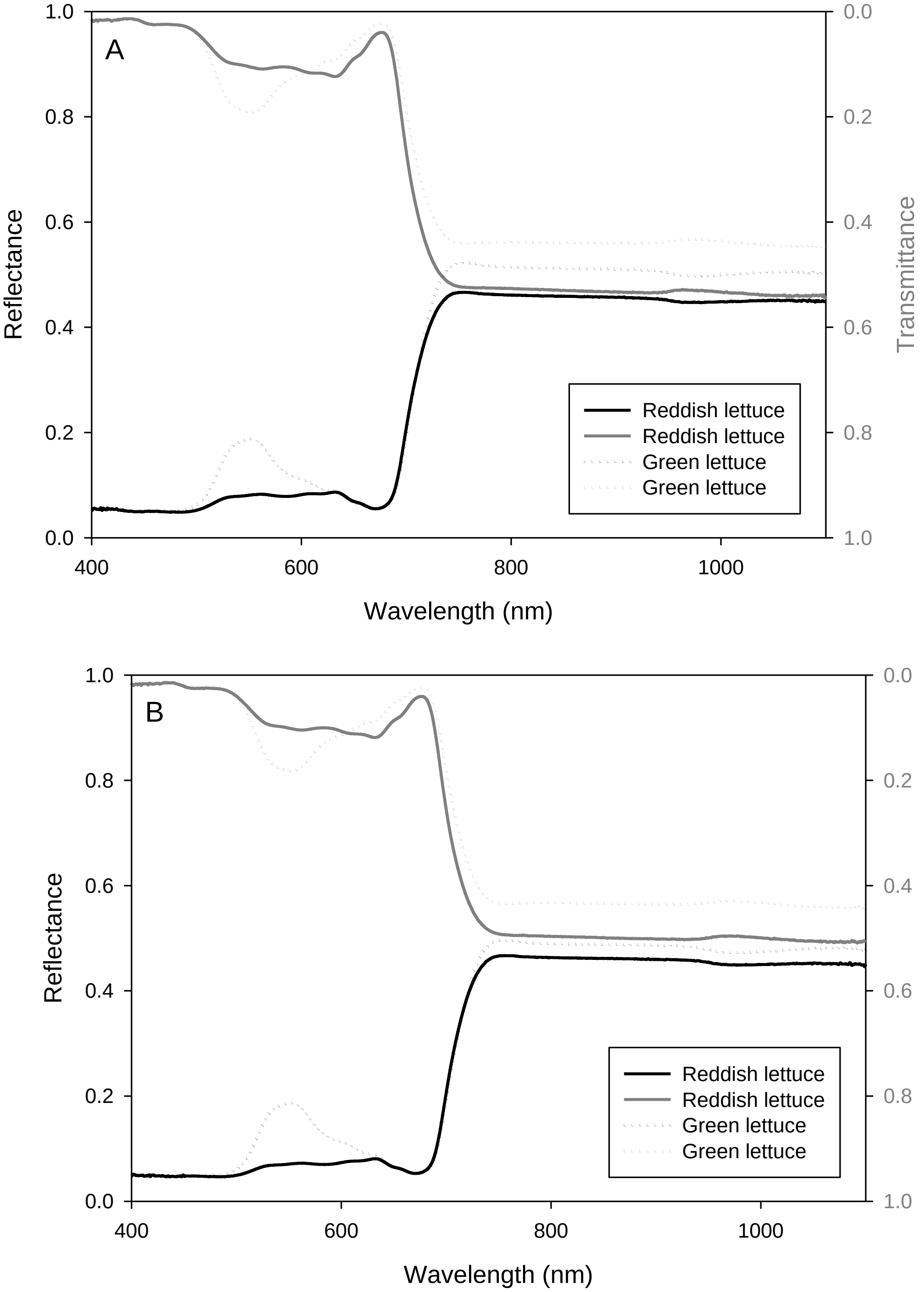
CONCLUSIONS

Spectral dependences of leaf absorptance and photosynthetic rate at a single leaf were similar to those of previous research. Light absorptances of all lettuce cultivars were higher in red and blue regions, but a little lower in green region: peaks in photosynthetic rate were observed at 650-660 nm in red region and at 400-410 nm in blue region. However, quantum yield at green region was not lower than those in the blue and red regions. In addition, reddish leave showed significantly higher light absorptance but lower photosynthetic rate than green leaves in the green region. These differences were considered due to the higher content of anthocyanin functioning as “green light filter”. Simulated results by canopy transmittance models showed that optical properties at a single leaf were not the same as those at crop canopy level. The spectral dependence of light absorptance at crop canopy level became weaker than those at a single leaf. And photosynthetic rate at green region at canopy level became higher than those at a single leaf. Light conversion efficiencies of red and blue LEDs were much higher than that of green LED. Therefore, although green LED showed a high photosynthetic rate at crop canopy level, the photosynthetic efficiency considering electrical energy consumption was lower than red or blue LED due to its lowlight conversion efficiency.

Appendix



Appendix 1. Leaf areas (A) and fresh weight (B) of the four lettuce cultivars at two stages.



Appendix 2. Reflectance and transmittance of reddish and green leaves of ChukMyeon (A) and ChiMa (B) lettuce cultivars.

ABSTRACT IN KOREAN

LED 를 이용하는 식물공장에서 작물의 광합성효율과 LED 의 소비 전기 에너지는 스펙트럼에 의해 영향을 받는다. 현재까지 광합성과 식물 잎의 광학적인 특성에 대한 기존의 연구들은 대부분 식물의 단입엽 수준에 제한되었다. 본 연구에서는 소비 전기 에너지를 고려했을 때 작물의 광합성 효율이 극대화되는 LED 파장을 선별하기 위해 4 가지 품종의 상추를 엽색에 따라 붉은색 품종과 초록색 품종으로 나누어 단일엽 수준에서 광합성 및 광학적인 특성을 측정하고 이를 광의 작물 군락 투과 모델을 이용하여 군락 전체 수준으로 확장시켜 보고자 하였다. 400-700nm 의 PAR 범위 내에 10nm 간격의 미세파장에 대해서 상추 단일엽에서의 광합성 속도와 각 파장의 LED 의 광전환 효율을 측정하였다. 또한 광합성 측정이 이루어진 잎에 대하여 파장에 따른 흡광도를 측정하였다. 이렇게 단일엽에서 측정된 정보를 군락 투과 모델을 이용하여 작물 군락 전체 수준으로 확장시켜보았다. 초록색 상추와 붉은색 상추는 PAR 전체 범위 내에서는 유사한 흡광도를 나타냈지만 550nm 인근에 초록색 영역의 파장에 대해선 붉은색 상추가 보다 높은 흡광도를 나타내었다. 단일엽에서 측정된 광합성 속도는 650-660nm(단위는 영문에서는 space 를 주시만 국문에서는 붙임), 400-410nm 에서 가장 높았으며 광자의 양자 수율은 650-660nm, 400-410nm 와 더불어 540-560nm 에서 가장 높은 값을 나타내었다. 초록색 영역의 파장에 대해서 광합성 속도와 양자 수율 모두 초록색 상추가 붉은색 상추에 비해 높은 것으로 나타났다. 초록색 영역의 파장에 대한 상추의 엽색에 따른 차이는 붉은색 상추에 높은 안토시아닌 함량과 연관되어있다. 작물 군락 전체 수준에서 파장이 흡광도에 미치는 영향은 단일 엽 수준에 비해 매우 감소하는 것으로 나타났다. 군락 전체 수준에서 초록색 영역의 파장의 흡광도는 빨간색이나

파란색 영역의 파장의 흡광도와 거의 유사한 것으로 나타났다. 초록색 영역 파장의 양자수율과 작물 전체에서의 흡광도가 빨간색이나 파란색 영역의 파장에 비해 낮지 않다는 결과에 의해 초록색 영역의 파장은 작물 군락 전체 수준에서 계산된 광합성 효율이 단일엽 수준에서 측정된 광합성 속도에 비해 증가하는 것으로 나타났다. 동일한 광도를 출력하는데 소비되는 LED 의 광전환효율은 초록색 영역 파장의 LED 가 빨간색과 파란색 영역 파장에 비해 매우 낮은 것으로 나타났다. 그 결과 초록색 영역 파장의 LED 는 높은 수준의 작물 군락 전체 수준에서의 광합성 효율에도 불구하고 소비 전기 에너지 대비 광합성 효율이 매우 낮은 것으로 나타났다. 이러한 작물 전체 군락 수준에서 계산된 결과는 단일엽 수준에서의 측정된 결과보다 광의 파장에 대한 작물의 실제 반응을 사실적으로 반영할 것이다. 또한 본 결과는 시설원예에서 인공광원 설계를 최적화하고 투입 에너지를 절감시키기 위한 보다 많은 정보를 제공할 수 있을 것이다.

주요어: 광분포, 광전환효율, 광질, 광투과 모델, 광학적 특성, 상추, 식물공장

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