



A THESIS FOR THE DEGREE OF MASTER OF SCIENCE

Enhanced Electron Transport and Photosynthetic Performance in Strawberry (*Fragaria* × *ananassa* Duch.) Grown Under Modified Sunlight by Spectrum Conversion Film

광전환 필름에 의하여 변형된 태양광 하에서 재배된 딸기의 향상된 전자전달 및 광합성 능력

BY

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THE GRADUATE SCHOOL OF SEOUL NATIONAL UNIVERSITY

Enhanced Electron Transport and Photosynthetic Performance in Strawberry (Fragaria × ananassa Duch.) **Grown Under Modified Sunlight by Spectrum Conversion Film**

UNDER THE DIRECTION OF DR. JUNG EEK SON SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF SEOUL NATIONAL UNIVERSITY

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ABSTRACT

Functional films have been used in greenhouses to improve the light environment for crop growth. Among these films, a spectrum conversion film converting the green light of incident sunlight into red light has been reported to increase the productivity of various crops. However, the results are not always consistent, and the reasons for the improvement are not fully understood. The objectives of this study were to reveal the cumulative effects of a green-tored spectrum conversion film (SCF) on the electron transport and photosynthetic performance of *Fragaria* × *ananassa* Duch. The photosynthetic efficiency, leaf optical properties, chlorophyll content, chlorophyll fluorescence, growth, and fruit qualities when the plant was grown under a transparent polyethylene film (PE) and the SCF were evaluated. The sunlight modified by SCF did not change the leaf optical properties and chlorophyll content but significantly increased the chlorophyll fluorescence parameters related to reduction end electron acceptors at the photosystem (PS) I acceptor side and the efficiency of electron transport. Without an increase in nonphotochemical quenching, the electron flows of PSII and PSI and the cyclic electron flow of leaves grown under SCF were significantly higher than those parameters when grown under PE. After 48 days after transplanting, the photosynthetic efficiency and photosynthetic rates of leaves and whole plants increased significantly under SCF compared to PE. The vegetative growth was not affected by the SCF, but the average fruit weight, sweetness, acidity, and firmness of Fragaria × ananassa Duch. grown under the SCF were significantly improved. These results indicated that sunlight modified by SCF stimulates electron flow without photoinhibition, improving photosynthetic capacity and fruit quality.

key words: Chlorophyll fluorescence, JIP analysis, Light spectrum, Photosystem, Strawberry

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INTRODUCTION

Light is an important environmental factor that determines the growth and quality of crops. Photosynthesis, growth, and yield of plants in greenhouses are known to increase when the light environment is efficiently changed (Long et al. 2006; Zhu et al. 2008; Shin et al. 2021). In general, the quantum yield for the photosynthetic rate is different for each wavelength within photosynthetically active radiation (PAR, 400-700 nm) (McCree, 1972). Red light has the highest quantum yield for photosynthesis and plays an important role in plant growth and development such as upregulation of enzymes and genes related to sugars, acids and bioactive components of fruit in strawberry (Kasperbauer et al. 2001; Casierra-Posada et al. 2011; Ilić et al. 2015; Shiukhy et al. 2015; Miao et al. 2016, 2017).

Spectrum conversion films (SCFs) have been used to manipulate the light quality in greenhouses, converting less active light into more active light based on the quantum yield (McCree, 1972), that is, absorbing blue and green light and emitting red light. Previous studies have reported that SCF increases the yield of various crops such as tomato, cucumber, strawberry, radish, and lettuce (Novoplansky et al. 1990; Hemming et al. 2006; Hidaka et al. 2008; Nishimura et al. 2012; Park et al. 2016). However, due to the energy conversion process, the SCF unavoidably reduces the light intensity in PAR compared to transparent films (Yoon et al. 2020b) and can decrease short-term photosynthetic rate. Some plants such as celery, tomato, and sweet potato did not change with the light quality caused by SCF (Nishimura et al. 2009; Kwon et al. 2013; Park et al. 2016). Unlike monochromatic light, the effects of complex changes to light quality by SCF are challenging to estimate. Therefore, to clarify these questions, changes in photosynthetic mechanisms by SCF are required.

A recent study reported the effects of SCF-modified sunlight on plant photosynthesis. In *Arabidopsis thaliana*, plants grown under SCF significantly increased the photosynthetic rate, which was accompanied by an increase in cyclic electron flow (CEF) (Li et al. 2017). Similarly, the SCF improved the photosynthetic capacity of sweet pepper over time after covering with the SCF and increased the chlorophyll fluorescence parameters related to the reduction of end acceptors at the PSI electron acceptor side (Yoon et al. 2020a). However, previous studies could not explain whether the photosynthetic acclimation induced by SCF was applicable to other crops during entire growing periods. The objective of this study was to reveal the cumulative effects of a green-tored SCF on the photosynthetic traits, growth, morphology, and fruit quality of *Fragaria* × *ananassa* Duch. plant. SCF-induced photosynthetic acclimation was evaluated using photosynthetic efficiency, leaf optical properties, chlorophyll content and chlorophyll fluorescence.

LITERATURE REVIEW

Spectrum conversion film (SCF) is a functional covering material that converts ultra-violet (UV) or green light into blue or red light. McCree. (1972) suggested the average photosynthetic response of various plants is different for each light wavelength. Based on this study, SCF converts solar spectrum from less efficient spectrum (UV and green light) to more efficient spectrum (blue and red light).

SCF can be divided into two categories: green-to-red SCF and UV-to-blue SCF. Each SCF has its advantages and disadvantages. UV-to-blue SCF has advantage of increasing the blue light without decreasing the photosynthetic photon flux density (PPFD), but the spectrum conversion efficiency is inefficient due to the low UVs in sunlight (Hemming et al. 2006). Green-to-red SCF has advantage of increasing the red light with the highest relative quantum yield for photosynthesis, but it has critical disadvantage of reducing the light quantity (Yoon et al. 2020b).

In the previous research, Hemming et al. (2006) reported that UV-to-blue SCF increased PAR transmittance compared to conventional clear film. The vegetative growth parameters, such as dry weight of leaves and leaf area, of strawberry plant grown under UV-to-blue SCF did not differ significantly (Hemming et al. 2006). However, UV-to-blue SCF significantly increased the leaf length and shoot dry weight of welsh onion (Hidaka et al. 2008). In case of tomatoes, UV-to-blue SCF significantly increased the number of fruits (Kwon et al. 2013).

Using green-to-red SCFs, the tomato fruit yields and the number of rose flowers significantly increased by 19.6% and 26.7%, respectively (Novoplansky et al. 1990). Hidaka et al. (2008) reported green-to-red SCF slightly increased leaf photosynthetic rate. Accordingly, root fresh weight of radish and shoot fresh weight were significantly increased compared to the clear film. However, fresh weight and morphology of celery, sweet potato, and spinach grown at SCF were not significantly different. However, the effect of each SCFs is species-specific. In the Arabidopsis pgr5 mutant, which lacks functions of the Proton Gradient Regulation 5 protein and inactivates the cyclic electron flow (CEF), photoinhibition was increased by aggravation of photodamage to PSII and prevention of the repair of photodamage (Takahashi et al. 2009). Li et al. (2017) suggested that wild-type Arabidopsis grown at green-to-red SCF has higher ATP/NADPH ratio through CEF, photosynthetic rates, and yield compared to the *pgr5* mutant. In addition, Yoon et al. (2020a) reported the photosynthetic efficiency and the maximum photosynthetic rates of sweet pepper grown at green-to-red SCF significantly increased over time after covering with such SCF. The authors also reported green-to-red SCF significantly promoted electron transfer around PSI, improving photosynthetic performance and growth of sweet pepper.

MATERIALS AND METHODS

Spectral characteristics and growth environment

Strawberry seedlings (*Fragaria* × *ananassa* Duch. cv. Seolhyang) were grown in a commercial nursery until 3–4 normal leaves appeared. On January 17, 2020, the seedlings were transplanted into pots (15 cm in diameter) in experimental greenhouses ($L \times W \times H$, $2 \times 3 \times 2$ m). Commercial growing media for strawberries (BC2, BVB, Alast, Netherlands) were used. The air temperature was set at 25/15 °C day/night with roof vents and hot-water pipe systems. After transplanting, the plants were supplied with nutrient solutions of electrical conductivity of 1.2–1.7 dS m⁻¹ and pH 5.5 for each growth stage.

The experimental greenhouses were covered with treatment films in a Venlo-type glass greenhouse at the experimental farm of Seoul National University, located in Suwon (37° 16' N, 126° 59' E), Korea. A polyethylene film (PE, Taekwangnewtec Co., Ltd., Seoul, Korea) and a spectrum conversion film (SCF) containing the fluorescent dye (developed by the Department of Materials and Engineering of Seoul National University, Korea) were used. The maximum absorption and emission spectra of the SCF dye were 582 and 620 nm, respectively (Fig. 1). The SCF was made by extrusion molding of the synthesized dye between films, and the PE was made in the same way but containing resin substance. The thickness of PE and SCF was the same at 100 μ m.



Fig. 1. Normalized absorption and emission spectra (a) and the chemical structure (b) of the dye used for spectrum conversion film. The absorption peaks were 448, 542, and 582 nm, and the emission peak was 620 nm.

Light intensity and temperature in each greenhouse were measured using a quantum sensor (SQ110, Apogee Instrument, Logan, UT, USA) and a datalogger (TR-71U, T&D Cor., Nagano, Japan) at the plant height level. Relative humidity was measured using an air quality monitor (AM-21, Wisesensing, Inc., Yongin, Korea). The spectral irradiance was measured using a spectroradiometer (BLUE-Wave spectrometer, StellarNet, Inc., Tampa, FL, USA) connected to a fiber optic cable with a light receptor (CR2, StellarNet, Inc.).

Optical properties of films and leaves

The transmittance of the films was measured at room temperature using a spectroradiometer connected to an integrating sphere (IC-2, StellarNet, Inc.) in the range of 280 to 980 nm. A solar simulator (XIL-01B50KPV1, SERIC Ltd., Tokyo, Japan) was used as a light source. The transmittance and reflectance of leaves were measured from 280 to 980 nm using a spectroradiometer. Nine leaves were randomly selected and measured from each treatment. The absorbance of leaves was calculated as 100 – transmittance – reflectance.

Chlorophyll content

Four plants were randomly selected from each treatment, and the leaves of the upper, middle, and bottom were harvested. Chlorophyll and carotenoid content was measured according to Porra's method (Porra et al. 1989). All leaf discs of 0.566 cm² were submerged in 1.5 ml *N*,*N*-dimethylformamide. Chlorophylls were extracted for 48 h at room temperature in the dark. The samples were vortexed and centrifuged at 10,000 rpm for 10 min at 25 °C before spectrophotometric analysis was carried out. Thereafter, the absorbance (*A*) of the solution was measured at 664, 647, and 480 nm using a spectrophotometer (Photolab 6100vis, WTW, Weilheim, Germany). Chlorophyll and carotenoid contents were determined as:

Chl $a = (12 * A_{664}) - (3.11 * A_{647})$

 $Chl \ b = (20.78 * A_{647}) - (4.88 * A_{664})$

 $Total \ carotenoids = (1000 * A_{480} - 1.12 * Chl \ a - 34.07 * Chl \ b)/245$

Chlorophyll fluorescence

Chlorophyll fluorescence transient, called the JIP test, was measured on younger, medium, and older leaves using a chlorophyll fluorescence meter (Handy PEA fluorometer, Hanstatech, King Lynn, UK) at 64 DAT. The middle part of each leaf was dark-adapted for 20 min using a leaf clip (HPEA/LC, Hansatech), with 20 replicates per treatment. The measurement was conducted using a saturating pulse of 1,500 μ mol m⁻² s⁻¹, a pulse duration of 1 s, and a fixed gain of $1 \times$. The parameters obtained from the JIP test were phenomenological energy fluxes for absorption (ABS), trapped energy flux (TR_0) , electron transport (ET_0) , and electron flux reducing end electron acceptors at the PSI acceptor side (RE_0) per measured area of samples, called excited cross-section (CS). Through the parameters obtained, the quantum yield for electron transport (φ_{Eo}), the efficiency to move an electron farther than $Q_A^ (\psi_{E_0})$, the quantum yield for reduction of end electron acceptors at the PSI acceptor side (φ_{Ro}), the performance indexes for energy conservation from exciton to the reduction of intersystem electron acceptors (PI_{abs}) and to the reduction of PSI end acceptors (PI_{total}), and the maximum quantum yield of PSII efficiency (F_{ν}/F_m) were calculated from the following equations:

$$\varphi_{Eo} = \frac{ET_0}{ABS'}, \quad \psi_{Eo} = \frac{ET_0}{TR_0}, \quad \varphi_{Ro} = \frac{RE_0}{ABS'}, \quad PI_{abs} = \frac{RE_0}{ABS} \cdot \frac{TR_0}{ABS - TR_0} \cdot \frac{ET_0}{TR_0 - ET_0}, \quad PI_{total} = PI_{abs} \cdot \frac{RE_0}{ET_0 - RE_0}, \quad F_v / F_m = \frac{(F_m - F_0)}{F_m}$$

The electron transport rates of PSI and PSII (ETRI and ETRII) and nonphotochemical quenching (NPQ) were measured on the third leaf from each treatment. The measurement was conducted in light curve mode using a Dual-PAM-100 measuring system (Dual PAM-100, Heinz Walz, Effeltrich, Germany) with software (Dual PAM v1.19). The light curve was determined with photosynthetic photon flux densities (PPFDs) of 0, 10, 18, 36, 94, 172, 214, 330, 501, 759, 1,178, and 1,455 µmol m⁻² s⁻¹ for 30 s duration. The saturation pulse was 10,000 µmol m⁻² s⁻¹ for 300 ms. The measurements were conducted at room temperature. The cyclic electron flow (CEF) was calculated as ETRI – ETRII. All measurements were conducted with four replicates per treatment.

Gas exchange measurement

The photosynthetic light response curve was measured using a portable photosynthetic system (LI-6400XT, Li-Cor, Lincoln, NE, USA) with a light emitting diode (LED) light source chamber (6400-02B, Li-Cor) at 8, 48, 56, and 131 days after transplanting (DAT). Except for 8 DAT, all gas exchange measurements were performed with a third fully expanded leaf from the top of the plant with three or four replicates. Before measurement, the leaves were

light-adapted at a PPFD of 1,000 μ mol m⁻² s⁻¹ for 15 min using a light chamber. The temperature, relative humidity, and CO₂ concentration in the LED chamber were set at 25 °C, 60%, and 400 μ mol mol⁻¹, respectively. PPFDs at 2,000, 1,500, 1,200, 900, 600, 400, 200, 100, 50, and 0 μ mol m⁻² s⁻¹ were used to construct the light response curve.

The photosynthetic rates of leaves were measured using a photosynthetic system with a clear chamber (6400-08, Li-Cor) under PE and SCF. Measured data were recorded every minute for 20 min with 10 replicates. The recorded photosynthetic rates were fitted to a rectangular hyperbola model according to previous studies (Thornley, 1976; Givnish, 1988; Lobo et al. 2013):

$$P_n = -R_d + \frac{P_{max} * I}{P_{max}/\theta + I}$$

where P_n is the net photosynthetic rate (µmol m⁻² s⁻¹), R_d is the dark respiration rate (µmol m⁻² s⁻¹), P_{max} is the maximum net photosynthetic rate (µmol m⁻² s⁻¹), I is the photosynthetic photon flux density (µmol m⁻² s⁻¹), and θ is the quantum yield at I = 0 µmol m⁻² s⁻¹.

The photosynthetic rates of the whole plants were measured using a CO_2/H_2O infrared gas analyzer (LI-840, Li-Cor). Nine plants grown were randomly selected for each treatment and adapted to 300 µmol m⁻² s⁻¹ PPFD under an artificial solar light source (PLS 700W, LG Electronics, Seoul, Korea) at room temperature for one day. Whole-plant photosynthesis was measured

using three adapted plants in a closed chamber ($L \times W \times H$, $100 \times 80 \times 50$ cm) connected to a CO₂/H₂O infrared gas analyzer with three replicates. The light source used for the measurement was an 8:1:1 ratio of red, blue, and white LEDs with 1,000 µmol m⁻² s⁻¹ PPFD. The whole plant photosynthetic rates were measured by calculating the rate of reduction of CO₂ from 1,000 to 200 µmol mol⁻¹. The soil respiration was measured by calculating the rate of increment of CO₂ from 380 to 1000 µmol mol⁻¹. The air leakage of the closed chamber was measured by calculating the rate of reduction of CO₂ for 24 h at 1,000 µmol mol⁻¹. The soil respiration and air leakage were 0.0982 and 0.017 µmol mol s⁻¹, respectively, and these values were used to calibrate the whole plant photosynthetic rate.

Growth and morphological parameters

Growth and morphological parameters such as leaf, stem, crown weight, number of leaves, stem length, and plant height were measured in three plants sampled at harvest (32, 53, 75, and 124 DAT). The dry weight of the plants was measured after drying in an oven at 70 °C for 72 h. The leaf area was calculated using ImageJ 1.49 image analysis software (National Institutes of Health, Bethesda, MD, USA). The SPAD value was measured using a chlorophyll meter (SPAD-502, Konica Minolta, Tokyo, Japan).

Fruit quality

Fruit yield per plant was measured with six plants. All fruits were harvested after fully ripening. Fruit weight was measured at each harvest. The color value $(L^*, a^*, and b^*)$ was measured (n = 72) using a colorimeter (CM-2600d, Konica Minolta, Tokyo, Japan). Before color measurement, calibration of the colorimeter was conducted according to the manufacturer's instructions. Three measurements were made per fruit, and the average reading was calculated for each treatment. The fruits from each treatment were randomly selected for firmness measurement (n=68). The firmness of fruit was measured at the equatorial plane of the fruit using a texture analyzer (CT-3, Brookfield Co., Middleborough, MA, USA) with a flat probe of 100 mm diameter at a speed of 2 mm s^{-1} and a strain of 5 mm (Bang et al. 2019). The firmness was measured by N. Juice extracted from each treatment (n = 200) was used to determine soluble sugar content using a refractometer (PAL-1, Atago, Tokyo, Japan) and expressed as ^oBrix. Acidity was measured using a fruit acidity meter (GMK 708, G-Won Hitech, Seoul, Korea) and expressed as the percentage of citric acid.

Statistical analysis

For all measurements, the means between treatments were compared via Student's *t*-test with each replicate at P < 0.05, 0.01, and 0.001. R software (R 3.6.2, R Foundation, Vienna, Austria) was used for the statistical analysis containing the regression analysis of the leaf photosynthetic rate.

RESULTS

Spectral characteristics and growth environment

The transmittance of SCF decreased at blue (400–500 nm) and green (500– 600 nm) wavelengths and increased at red (600–700 nm) wavelengths compared to PE (Fig. 2a). The photon flux density under the SCF was decreased by 28% at the blue and green wavelengths compared to the PE (Fig. 2b and Table 1). The red and far-red (700–800 nm) wavelengths of SCF were increased by 7% and 5%, respectively, compared to PE. The red and far-red (R:FR) ratios at the PE and SCF were 1.27 and 1.30, respectively. The ratio of red to blue light (R:B) under SCF was 1.33 and higher than the ratio under PE (R:B = 1.00). The PPFD under the SCF was decreased by 17% compared to the PE at the experimental site.

Growth environment conditions during the growth period are shown in Table 2. The daily light integral (DLI) under the SCF was decreased by 25% compared to the DLI under the PE. The average daytime temperature under the SCF was decreased by 6% compared to the PE but not significantly. The average nighttime temperatures under PE and SCF were 13.4 and 13.3 °C, respectively.



Fig. 2. The spectral transmittance of films (a) and spectral irradiance (b) under the polyethylene (PE) film and spectrum conversion film (SCF) were measured at the experimental site at 12:00 on December 26, 2019.

Table 1. The spectral irradiance under the greenhouses (PE and SCF) in the experimental site at 12:00 on December 26, 2019.

	Spectral irradiance (µmol m ⁻² s ⁻¹)									
Film [–]	Blue (400–500 nm)	Green (500–600 nm)	Red (600–700 nm)	Far-red (700–800 nm)	PAR (400–700nm)	R:FR ratio ^z	R:B ratio ^y			
PE	349	394	349	275	1092	1.27	1			
SCF	281	297	374	288	952	1.30	1.33			

^zThe R:FR ratio is calculated by dividing Red into Far-red.

^yThe R:B ratio is calculated by dividing Red into Blue.

Film	Daily light integral (mol m ⁻² d ⁻¹)	Average photosynthetic photon flux density (µmol m ⁻² s ⁻¹)	Daytime air temperature (°C)	Nighttime air temperature (°C)	Relative humidity (%)
PE	9.55±4.33 ^{zy}	221±100	24.3±0.7	13.4±0.2	40.5
SCF	7.67±3.54	177±82	22.9±1.5	13.3±0.2	40±3

Table 2. Environmental conditions under the polyethylene (PE) film and spectrum conversion film (SCF) from February 10to May 8, 2020.

^zMean \pm SD, n = 131

^yAll data were not significantly different according to the *t*-test (P < 0.05).

Leaf optical properties and chlorophyll contents

The transmittance and reflectance of leaves were not different between the treatments (Fig. 3a). Accordingly, the absorbance of leaves was not different (Fig. 3b). The Chl a, Chl b, total Chl content, carotenoid content, and Chl a/b ratio were not significantly different between the treatments (Fig. 4).



Fig. 3. Leaf optical properties of *Fragaria* \times *ananassa* Duch. at 86 days after transplanting. Spectral transmittance (a) and reflectance (b) were used to calculate the spectral absorbance (c). The values were the mean of three replicates.



Fig. 4. Chlorophyll and carotenoid content of *Fragaria* × *ananassa* Duch. leaves grown under polyethylene (PE) film and spectrum conversion film (SCF) at 86 days after transplanting. The vertical bars indicate 1SD; n=3. The asterisks indicate significant differences (Student's *t*-test, *P < 0.05, **P< 0.01, ***P < 0.001).

Chlorophyll fluorescence transient

The chlorophyll fluorescence parameters of leaves under SCF were significantly increased compared to the chlorophyll fluorescence parameters of leaves under PE, except for younger leaves (Fig. 5). In the medium leaves, the performance indexes for energy conservation from exciton to the reduction of intersystem electron acceptors (PI_{abs}) and to the reduction of PSI end acceptors (PI_{total}), the quantum yield for electron transport (φ_{Eo}), the efficiency to move an electron farther than Q_A^- (ψ_{Eo}), and electron flux reducing end electron acceptors at the PSI acceptor side (RE₀/CS) were significantly increased under the SCF compared to the PE (Fig. 5b). In the older leaves, φ_{Eo} and ψ_{Eo} were significantly increased under SCF compared to PE (Fig. 5c).

The electron transport rates of PSII (ETRII) and PSI (ETRI) increased in the form of a saturation curve with the light intensity (Fig. 6a, b). The ETRII of leaves grown under the SCF was significantly increased above 759 μ mol m⁻² s⁻¹ PPFD. The ETRI and CEF in the SCF significantly increased above 214 μ mol m⁻² s⁻¹ PPFD rather than PE (Fig. 6b, c). The NPQ in the SCF was not different from the NPQ in the PE (Fig. 6d).



Fig. 5. Chlorophyll fluorescence parameters of younger (a), medium (b), and older (c) leaves of *Fragaria* × *ananassa* Duch. grown under polyethylene (PE) film and spectrum conversion film (SCF) at 64 days after transplanting with 20 replicates. Each parameter obtained from JIP-test analyses was normalized to that parameter of PE in the plot. The asterisks indicate significant differences (Student's *t*-test, *P < 0.05, **P < 0.01, ***P < 0.001).



Fig. 6. Electron transport rate of PSII (ETRII) and PSI (ETRI), cyclic electron flow (CEF), and nonphotochemical quenching (NPQ) of *Fragaria* × *ananassa* Duch. leaves grown under polyethylene (PE) film and spectrum conversion film (SCF) at 123 days after transplanting. The vertical bars indicate 1SD; n=4. The asterisks indicate significant differences (Student's *t*-test, *P < 0.05, **P < 0.01, ***P < 0.001).

Photosynthesis

The difference in photosynthetic rate between PE and SCF significantly and gradually increased over time (Fig. 7). At 8 DAT, the photosynthetic rate was not significantly different. The photosynthetic rates in the SCF at 48 DAT were significantly greater than the photosynthetic rates in the PE above a PPFD of 200 μ mol m⁻² s⁻¹. At 56 DAT, the differences in photosynthetic rate were significant at 900 and 2,000 μ mol m⁻² s⁻¹. At 131 DAT, the photosynthetic rates in the PE above 50 PPFD μ mol m⁻² s⁻¹.

The leaf photosynthetic rates in the SCF were higher than the leaf photosynthetic rates in the PE as the PPFD increased (Fig. 8a). From the regressed models, the maximum photosynthetic rates (P_{max}) under PE and SCF were 25 and 27 µmol m⁻² s⁻¹, respectively. The dark respiration (R_d) under the SCF was 4 µmol m⁻² s⁻¹, 225% lower than the R_d under PE. The quantum yields (θ) of PE and SCF were 0.11 and 0.05, respectively. With increasing CO₂ concentration, the photosynthetic rates increased, and the photosynthetic rates under the SCF increased significantly by approximately 20% (Fig. 8b).



Fig. 7. Light response curves of photosynthetic rates in the third fully expanded leaves of *Fragaria* × *ananassa* Duch. grown under polyethylene film (PE) and spectrum conversion film (SCF) at 8 (a), 48 (b), 56 (c), and 131 (d) days after transplanting. The vertical bars indicate 1SD; n=3-4. The asterisks indicate significant differences (Student's *t*-test, *P < 0.05, **P < 0.01, ***P < 0.001).



Fig. 8. Leaf photosynthetic rates (a) in the third expanded leaf at 102 days after transplanting and whole plant photosynthetic rates (b) of *Fragaria* × *ananassa* Duch. grown under polyethylene (PE) film and spectrum conversion film (SCF) 66 days after transplanting. The vertical bars indicate 1SD; n=3. The asterisks indicate significant differences (Student's *t*-test, *P < 0.05, **P < 0.01, ***P < 0.001).

Growth, morphology and fruit quality

Growth and morphological parameters, except for leaf area and stem length, were not significantly different between the treatments (Table 3). The longest stem length under the SCF at 53 DAT was significantly longer than the longest stem length under the PE at 53 DAT. The shoot dry weight in the SCF at 124 DAT increased by 10.5% but was not significantly different. The leaf area in the SCF was significantly increased by 15% at 124 DAT. The individual fruit weight under the SCF was increased by 16.1% compared to the individual fruit weight under the PE (Table 4). The fruit yield per plant and color values (L*, a*, b*) were not significantly different. The fruit juice under SCF had 12.9% lower acidity and 3.6% higher sweetness than PE. The firmness of SCF significantly increased by 10.5% compared to the firmness of PE.

DAT	T '1	Dry weight (g)				NT 61	T C (2)			
DAT	Film	Leaf	Stem	Crown	Shoot	No. of leaves	Leaf area (cm ²)	Stem length (cm)	Plant height (cm)	SPAD value
32	PE	2.4±0.32 ^z	0.5±0.06	0.4±0.05	3.4±0.42	21±2	578±90	14.9±0.78	19.0±1.66	40.0±1.09
	SCF	2.4±0.20	0.5 ± 0.04	0.3±0.05	3.2±0.27	18±2	591±49	16.5±0.39	19.0±1.68	40.6±0.44
53	PE	6.7 ± 0.58	1.6±0.18	0.9 ± 0.06	9.2±0.79	42±2	1429±92	21.3±0.48	25.2±2.50	39.5±0.67
	SCF	7.4±0.52	1.9±0.13	1.0 ± 0.05	10.3±0.60	39±2	1575±69	$24.0 \pm 1.10^{*y}$	27.4±1.96	40.0±0.62
75	PE	19.2±0.30	4.5±0.11	2.3±0.55	26.1±0.78	59±4	2395±219	22.3±2.40	30.4±1.55	42.7±0.51
	SCF	18.0±3.04	4.3±0.80	2.6±0.27	24.9±4.10	58±9	2786±496	22.7±2.37	30.7±1.15	43.3±0.61
124	PE	20.7±6.68	5.6±2.07	4.3±1.81	30.7±10.45	70±18	3673±561	24.5±2.43	30.6±3.55	40.7±1.39
	SCF	28.7±2.49	7.9±1.19	5.4±0.97	42.1±4.27	99±12	4341±401*	24.4±2.59	31.9±1.61	40.2±0.69

Table 3. Growth and morphology of *Fragaria* × *ananassa* Duch. under polyethylene (PE) film and spectrum conversion film (SCF) at 32, 53, 75, and 124days after transplanting (DAT).

^zMean \pm SD, n = 3.

^ySignificant difference according to *t*-test (P < 0.05) is marked with asterisk.

Table 4. Fruit quality of *Fragaria* × *ananassa* Duch. grown under polyethylene (PE) film and spectrum conversion film (SCF) from March 29 to May 29, 2020.

Film	Yield (g/plant)	Fruit weight (g/fruit)	L*	a*	b*	Acidity (%)	Sweetness (Brix)	Sugar/acid ratio	Firmness (N)
PE	287.0±18.54 ^z	11.8±0.25	34.0±4.05	46.4±5.87	43.8±13.26	1.0±0.19	9.2±1.41	10.3±4.44	7.2±1.34
SCF	300.6±23.81	14.0±0.30***y	34.3±4.23	47.5±5.51	45.3±13.33	0.8±0.21***	9.5±1.55**	12.3±6.79**	8.1±2.26***

²Mean \pm SD, n = (Yield = 6, Fruit weight = 500, color = 72, Acidity = 127, Sweetness = 200, Sugar/acid ratio = 127, Firmness = 68).

^ySignificant difference according to *t*-test is marked with asterisk (*, P < 0.05; **, P < 0.01; ***, P < 0.001).

DISCUSSION

Light environment and photosynthetic efficiency

Light intensity is one of the most important factors for plant photosynthetic efficiency as well as growth (Splinter, 1974; Vasseur et al. 2011; Kang et al. 2013). Pons and De Jong-Van Berkel (2004) reported a significant decrease in photosynthetic efficiency and capacity in six plants grown under a shade filter for a week. In this study, the SCF had low transmittance in the range of PAR, reducing the average PPFD, daily light integral, and air temperature (Table 2). Nevertheless, the increases in photosynthetic efficiency and capacity of Fragaria × ananassa Duch. leaves grown under the SCF were maintained after a certain period, resulting in improvement of photosynthetic rates under natural light as well as artificial lighting (Figs. 7 and 8). This result is consistent with the increase in photosynthetic efficiency of Arabidopsis and sweet pepper grown for a long time under SCF despite reduced light intensity (Li et al. 2017; Yoon et al. 2020a). These results suggested that photosynthetic acclimation was caused by light quality but not light intensity. Photosynthetic acclimation to light quality includes changes in chlorophyll content, leaf optical properties, electron transport, and gene expression related to photosynthetic mechanisms (Murchie and Horton, 1998; Dietzel et al. 2008; Zheng and Van Labeke, 2017; Yang et al. 2018; Kalaitzoglou et al. 2019).

Red light has the highest quantum yield for photosynthesis, but monochromatic red light can severely damage the plant photosynthetic apparatus due to 'red light syndrome' (Trouwborst et al. 2016; Miao et al. 2019). This 'red light syndrome' could be alleviated by adding blue light (Miao et al. 2019). In this study, the SCF increased the R:B ratio (Table 1). Similarly, Shengxin et al. (2016) indicated that the net photosynthetic rate of rapeseed grown under R:B = 3:1 was higher than the net photosynthetic rate under R:B= 1:1. Blue light has the second highest quantum yield sensed by cryptochromes and phototropins and promotes the synthesis of chlorophyll a (Sæbø et al. 1995; Wang et al. 2016; Zheng and Van Labeke, 2017). In addition, tomatoes grown in blue light showed lower electron transfer rates and higher CEF-inducing NPQ than tomatoes grown in red light (Yang et al. 2018). Green light has the lowest quantum yield but has a high transmittance and increases canopy photosynthesis (Paradiso et al. 2011; Lee et al. 2017). Green light also affects morphological changes such as hypocotyls, stem elongation, and leaf expansion by shade avoidance syndrome (Folta and Maruhnich, 2007; Zhang et al. 2011). However, these responses are the monochromatic effect of each light, so the effect of increased or decreased light quality by SCF is difficult to estimate.

Chlorophyll content and leaf optical properties

For the light absorption of *Fragaria* \times *ananassa* Duch. leaves, it is intriguing that similar chlorophyll content and leaf optical properties grew under PE and SCF (Figs. 3 and 4). Chlorophyll content is directly affected by light intensity and quality (Sæbø et al. 1995; Hoffmann et al. 2015). The total chlorophyll content increased as the light intensity decreased in chrysanthemum and strawberry (Zheng and Van Labeke 2018; Zheng et al. 2019). The biosynthesis of photosynthetic pigments is also regulated by light quality. Blue light is generally known to be favorable for the synthesis of chlorophyll a (Sæbø et al. 1995; Wang et al. 2016; Zheng and Van Labeke, 2017). In detail, blue light improved the expression of MgCH, GluTR, FeCH, and the enzymes that regulate chlorophyll synthesis (Wang et al. 2009; Fan et al. 2013). The carotenoid content was also increased by additional blue light. Fu et al. (2013) reported that the combination of blue and red light enhanced Chl b and carotenoid biosynthesis in green microalgae compared to pure red light. However, red light suppressed chlorophyll synthesis because the red light downregulated the protein and/or gene expression of enzymes involved in the biosynthesis of tetrapyrroles (Sood et al. 2005). However, in this study, despite the decreases in 23% light intensity and 24% blue light by the SCF, the Chl a, Chl b, Chl a/b ratio and carotenoid content remained unchanged (Fig. 4). The changes in light intensity and quality in the SCF may not be enough to change the chlorophyll content and SPAD value. Finely modified sunlight by SCF did not change the chlorophyll content, and therefore, the optical properties of

leaves did not change. In basil plants grown at R:B ratios of 0.5, 1.0, and 2.0, chlorophyll and carotenoid contents increased, but not significantly (Lobiuc et al. 2017).

Electron transport from PSII to PSI

Chlorophyll fluorescence parameters are reliable biomarkers for evaluating electron transport at the level of the photosynthetic apparatus (Kalaji et al. 2018). Based on the JIP test, the parameters represent the quantification of energy flow through PSII and PSI (Strasser et al. 2006). Since the JIP test is measured after dark adaptation, the maximal efficiency can be evaluated. In this study, chlorophyll fluorescence parameters of younger leaves of Fragaria \times ananassa Duch. showed no significant difference (Fig. 5). Because either the photosynthetic apparatus was not fully developed (Sitko et al. 2020) or photosynthetic acclimation did not yet occur, we assume that the younger leaves under the PE and SCF had similar photosynthesis capacities. In the medium leaves with relatively vigorous photosynthetic capacity, ABS/CS, TR₀/CS, and ET₀/CS under the SCF were similar, but RE₀/CS were significantly increased, similar to a previous study (Yoon et al. 2020a). Therefore, the energy fluxes for absorption, trapping, and electron transport were not changed but the reduction of the PSI acceptor side increased. Significant increases in φ_{Eo} and ψ_{Eo} mean an increase in electron transport,

indicating a significant increase in the electron transport efficiency of PSII. The performance index PI describes the energy conservation from photons absorbed by PSII to the reduction of intersystem electron acceptors (PI_{abs}) and to the reduction of PSI end acceptors (PI_{total}). Therefore, PI is the most powerful and comprehensive parameter due to its sensitivity in quantifying the effects of abiotic factors on photosynthetic performance in many studies (Tsmilli-Michael and Strasser, 2008; Jedmowski et al. 2014; Ceusters et al. 2019; Galic et al. 2019, Tsimilli-Michael, 2019). In this study, although ABS/CS, TR₀/CS, and ET₀/CS were unchanged, the SCF treatment significantly increased PI_{abs} due to the increases in ϕ_{Eo} and ψ_{Eo} . In addition, increased PI_{total} indicates that the SCF facilitated electron transport from excitons to the reduction of PSI end acceptors, thereby increasing photosynthetic capacity.

As the leaves were light-adapted, the electron flows in PSII and PSI increased in the SCF (Fig. 6). Both the chlorophyll fluorescence results in darkadapted and light-adapted leaves suggest that sunlight modified by SCF had an effect on electron flow around PSI. CEF is an alternative electron transport pathway that circulates electrons from the ferredoxin of PSI back to the electron transport chain (Kramer et al. 2004; Shikanai, 2014; Nawrocki et al. 2019). In general, CEF is known to activate photoprotection by producing additional ATP without NADPH accumulation to protect the photosystem in a fluctuating light environment (Yamori et al. 2015; Shikanai and Yamamoto, 2016). However, far-red irradiation of leaves drives CEF around PSI (Kono et al. 2017; 2020; Wang et al. 2020). In this study, the far-red irradiance in the SCF was approximately 4% greater than the far-red irradiance in the PE (Table 1). Additionally, an appropriately increased ATP/NADPH ratio can accelerate the Calvin-Benson cycle (Osmond et al. 1981; Kramer et al. 2004). Controlling the ATP/NADPH ratio through the CEF at low light intensities might be favorable for Calvin-Benson cycle activity (Yamori et al. 2011; 2015; Huang et al. 2015; Laisk et al. 2007; 2010; Li et al. 2017). In this study, CEF was increased significantly by SCF, consistent with previous research in Arabidopsis (Li et al. 2017). The Arabidopsis *pgr5* mutant lacks the functions of the proton gradient regulation 5 protein and inactivates CEF. WT Arabidopsis grown in SCF had a higher ATP/NADPH ratio, photosynthetic rates, and plant yield than the *pgr5* mutant grown in green-to-red SCF (Li et al. 2017).

NPQ is caused by CEF, which prevents too many electrons from being transported to PSI and results in photoinhibition (Munekage et al. 2004; Takahashi et al. 2009; Yamori et al. 2015; Yang et al. 2018; Kono et al. 2020). However, NPQ in the SCF was not significantly increased (Fig. 6d) because it is assumed that the electron transport of acclimated leaves under the SCF was not sufficiently excessive to induce photoinhibition. Across all data, modified sunlight increased the electron flow of PSI and CEF and improved photosynthetic performance without stress.

Vegetative and reproductive growth

Light quality can determine photomorphogenesis as well as the growth of plants. In this study, *Fragaria* \times *ananassa* Duch. grown under SCF did not significantly increase vegetative growth parameters, excluding leaf area and stem length, despite the increased photosynthetic capacity. In general, leaf area is regulated by PhyB, which reacts to light near 660 nm (Klose et al. 2015; Yoshida et al. 2018). The increases in red light by SCF may stimulate PhyB. These results are consistent with a previous study, which showed that the leaf area of tomatoes and cucumbers grown under SCF was increased (Park et al. 2016). Stem length at 53 DAT was promoted in the SCF but was not maintained at 75 and 124 DAT. Yoon et al. (2020a) reported that the initial effect of SCF on some morphological parameters was not maintained until the end of the growth period. In contrast, the total and leaf fresh weight of plants such as cucumber, tomato, celery, and Welsh onion grown under SCF significantly increased (Hidaka et al. 2008; Nishimura et al. 2012; Park et al. 2016).

Vegetative and reproductive growth are generally affected by the photosynthetic rate (Zhu et al. 2007; Zhu et al. 2010; Li et al. 2014; Ort et al. 2015; Simkin et al. 2019). The increased photosynthetic rate using supplemental lighting increased fruit weight, sweetness, and the number of fruits of strawberries and tomatoes (Hidaka et al. 2013, 2014, 2015; Pan et al. 2019). Interestingly, despite the unchanged vegetative growth, the quality of

the fruit grown under the SCF was improved (Tables 3 and 4). These results agreed with González et al. (2003) and Hemming et al. (2006), who reported that the subtle change in solar spectrum by SCF did not affect vegetative growth but increased fruit dry weight and yield in strawberries. However, none of them, including this study, investigated root weight. Zheng et al. (2019) reported that strawberry seedlings with higher photosynthetic rates had higher root dry weights. Therefore, consideration of the root weight of plants is required.

In this study, the SCF increased red light by 7% and far-red light by 5% compared to the PE, but since the SCF also increased the R:FR ratio, it is necessary to study whether the effect of far-red to fruit is dominated by the absolute amount of far-red or the far-red fraction (Kusuma and Bugbee, 2020). Recently, increased far-red light by supplemental lighting has been found to upregulate key enzymes and genes related to fruit sugar transportation and metabolism and elevate the fruit sink strength of tomato (Ji et al. 2020). In particular, strawberries grown using a red mulching film, which reflects red and far-red light, had higher levels of *FaSPS* expression, sucrose synthase activity, sucrose phosphate synthase activity, and sweetness/acidity ratio than a white mulching film (Miao et al. 2017). Sucrose is a primary sugar of most strawberry cultivars and is the main form of photosynthate translocated into the fruits. In this study, whether the high sweetness and low acidity of fruits under the SCF was due to the increased far-red and/or the increased photosynthesis was not

revealed exactly. Further study is needed to explain the exact effects of modified sunlight through SCF on fruit quality.

CONCLUSION

This study demonstrated the effects of a spectrum conversion film (SCF) on growth and fruit quality in *Fragaria* × *ananassa* Duch. and focused on revealing the reasons for increased photosynthesis using chlorophyll fluorescence. The increased red and far-red light by SCF over a long time led to higher photosynthetic efficiency, while SCF did not affect the photosynthetic chlorophyll content or leaf optical properties. Regarding chlorophyll fluorescence parameters, SCF increased the efficiency of electron transport from PSII to the intersystem electron transport chain (φ_{Eo} and ψ_{Eo}) of leaves. In particular, the parameters related to PSI electron transport (RE₀/CS, PI_{total}, ETRI and CEF) were significantly increased by the SCF. Fruit qualities such as fruit weight, sweetness, sweet/acid ratio, and firmness were promoted under the SCF. These results suggest that the SCF-induced enhancement of electron transport around PSI as well as PSII promotes photosynthetic performance and improves fruit quality.

LITERATURE CITED

- Bang J, Lim S, Yi G, Lee JG, Lee EJ (2019) Integrated transcriptomicmetabolomic analysis reveals cellular responses of harvested strawberry fruit subjected to short-term exposure to high levels of carbon dioxide. Postharvest Biol Technol 148: 120–131.
- Casierra-posada F, Fonseca E, Vaughan G (2011) Fruit quality in strawberry (*Fragaria* sp.) grown on colored plastic mulch. Agron Colomb 29: 407–413.
- Ceusters N, Valcke R, Frans M, Claes JE, Van den Ende W, Ceusters J (2019) Performance index and PSII connectivity under drought and contrasting light regimes in the CAM Orchid *Phalaenopsis*. Front Plant Sci 10: 1–15.
- Dietzel L, Bräutigam K, Pfannschmidt T (2008) Photosynthetic acclimation: State transitions and adjustment of photosystem stoichiometry - Functional relationships between short-term and long-term light quality acclimation in plants. FEBS Journal 275: 1080–1088.
- Fan X, Zang J, Xu Z (2013) Effects of different light quality on growth, chlorophyll concentration and chlorophyll biosynthesis precursors of nonheading Chinese cabbage (*Brassica campestris* L.). Acta Physiol Plant 35: 2721–2726.
- Folta K, Maruhnich S (2007) Green light: A signal to slow down or stop. J Exp Bot 58: 3099–3111.
- Fu W, Guðmundsson Ó, Paglia G (2013) Enhancement of carotenoid biosynthesis in the green microalga Dunaliella salina with light-emitting diodes and adaptive laboratory evolution. Appl Microbiol Biotechnol 97: 2395–2403.

- Galic V, Franic M, Jambrovic A, Ledencan T, Brkic A, Zdunic Z, Simic D (2019) Genetic correlations between photosynthetic and yield performance in maize are different under two heat scenarios during flowering. Front Plant Sci 10: 1-11.
- Givnish T (1988) Adaptation to sun and shade: a whole-plant perspective. Funct Plant Biol 15:63.
- González A, Rodríguez R, Bañón S, Franco JA, Fernández JA, Salmerón, A, Espí E (2003) Strawberry and cucumber cultivation under fluorescent photoselective plastic films cover. Acta Hortic. 614: 407–413.
- Hemming S, Van Os E, Hemming J, Dieleman J (2006) The effect of new developed fluorescent greenhouse films on the growth of *Fragaria x ananassa* "Elsanta". Eur J Hortic Sci 71: 145–154.
- Hidaka K, Yoshida K, Shimasaki K (2008) Spectrum conversion film for regulation of plant growth. J Fac Agric Kyushu Univ 53: 549–552.
- Hidaka K, Dan K, Imamura H (2013) Effect of supplemental lighting from different light sources on growth and yield of strawberry. Environ Control Biol 51: 41–47.
- Hidaka K, Okamoto A, Araki T, Miyoshi Y, Dan K, Imamura H, Kitano M, Sameshima K, Okimura M (2014) Effect of photoperiod of supplemental lighting with light-emitting diodes on growth and yield of strawberry. Environ Control Biol 52: 63–71.
- Hidaka K, Dan K, Imamura H, Takayama T, Sameshima K, Okimura M (2015)
 Variety comparison of effect of supplemental lighting with LED on growth and yield in forcing culture of strawberry. Environ Control Biol 53: 135– 143.

- Hoffmann A, Noga G, Hunsche M (2015) High blue light improves acclimation and photosynthetic recovery of pepper plants exposed to UV stress. Environ Exp Bot 109: 254–263.
- Huang W, Yang YJ, Hu H, Zhang SB (2015) Different roles of cyclic electron flow around photosystem I under sub-saturating and saturating light intensities in tobacco leaves. Front Plant Sci 6: 1–9.
- Ilić, Z, Milenković L, Šunić L, Fallik E (2015) Effect of coloured shade-nets on plant leaf parameters and tomato fruit quality. J Sci Food Agric 95: 2660–2667.
- Jedmowski C, Bayramov S, Brüggemann W (2014) Comparative analysis of drought stress effects on photosynthesis of Eurasian and North African genotypes of wild barley. Photosynthetica 52: 564–573.
- Ji Y, Nuñez Ocaña D, Choe D, Larsen DH, Marcelis LFM, Heuvelink E (2020) Far-red radiation stimulates dry mass partitioning to fruits by increasing fruit sink strength in tomato. New Phytol 228.
- Kalaitzoglou P, van Ieperen W, Harbinson J, van der Meer M, Martinakos S, Weerheim K, Nicole CCS, Marcelis LFM (2019) Effects of continuous or end-of-day far-red light on tomato plant growth, morphology, light absorption, and fruit production. Front Plant Sci 10: 1–11.
- Kalaji HM, Rastogi A, Živčák M, Brestic M, Daszkowska-Golec A, Sitko K, Alsharafa KY, Lotfi R, Stypiński P, Samborska IA, Cetner MD (2018)
 Prompt chlorophyll fluorescence as a tool for crop phenotyping: an example of barley landraces exposed to various abiotic stress factors. Photosynthetica 56: 953–961.
- Kang JH, KrishnaKumar S, Atulba S, Jeong BR, Hwang SJ (2013). Light intensity and photoperiod influence the growth and development of

hydroponically grown leaf lettuce in a closed-type plant factory system. Hortic Environ Biotechnol 54: 501–509.

- Kasperbauer M, Loughrin J, Wang S (2001) Light reflected from red mulch to ripening strawberries affects aroma, sugar and organic acid concentrations. Photochem Photobiol 74: 103–107.
- Klose C, Venezia F, Hussong A, Kircher S, Schäfer E, Fleck C (2015) Systematic analysis of how phytochrome B dimerization determines its specificity. Nat Plants 1: 15090.
- Kono M, Yamori W, Suzuki Y, Terashima I (2017) Photoprotection of PSI by far-red light against the fluctuating light-induced photoinhibition in Arabidopsis thaliana and field-grown plants. Plant Cell Physiol 58: 35–45.
- Kono M, Kawaguchi H, Mizusawa N, Yamori W, Suzuki Y, Terashima I (2020) Far-red light accelerates photosynthesis in the low-light phases of fluctuating light. Plant Cell Physiol 61: 192–202.
- Kramer D, Avenson T, Edwards G (2004) Dynamic flexibility in the light reactions of photosynthesis governed by both electron and proton transfer reactions. Trends Plant Sci 9: 349–357.
- Kusuma P, Bugbee B (2020) Far-red fraction: an improved metric for characterizing phytochrome effects on morphology. J Am Soc Hortic Sci J: 1–11.
- Kwon JK, Park KS, Choi HH, Lee SY, Bekhod K, Hwang MR, Kang NJ (2013) Growth and Developmental Characteristics of Lettuce, Tomato and Melon Grown under Spectrum Conversion Greenhouse Films. J Agric Life Sci 47:57–63.

- Laisk A, Eichelmann H, Oja V, Talts E, Scheibe R (2007) Rates and roles of cyclic and alternative electron flow in potato leaves. Plant Cell Physiol 48: 1575–1588.
- Laisk A, Talts E, Oja V, Eichelmann H, Peterson R (2010) Fast cyclic electron transport around photosystem I in leaves under far-red light: A protonuncoupled pathway? Photosynth Res 103: 79–95.
- Lee JW, Kang WH, Park KS, Son JE (2017) Spectral dependence of electrical energy-based photosynthetic efficiency at single leaf and canopy levels in green- and red-leaf lettuces. Hortic Environ Biotechnol 58: 111–118.
- Li T, Heuvelink E, Dueck TA, Janse J, Gort G, Marcelis LFM (2014) Enhancement of crop photosynthesis by diffuse light: Quantifying the contributing factors. Ann Bot 114: 145–156.
- Li Y, Tu W, Liu C, Liu W, Hu G, Liu X, Chen Z, Yang C (2017) Light conversion film promotes CO₂ assimilation by increasing cyclic electron flow around PhotosystemI in Arabidopsis thaliana Int J Hydrog Energy 42: 8545–8553.
- Lobiuc A, Vasilache V, Pintilie O, Stoleru T, Burducea M, Oroian M, Zamfirache MM (2017) Blue and red LED illumination improves growth and bioactive compounds contents in acyanic and cyanic *Ocimum basilicum* L. Microgreens. Molecules 22:2111.
- Lobo F de A, de Barros MP, Dalmagro HJ, et al (2013) Fitting net photosynthetic light-response curves with Microsoft Excel a critical look at the models. Photosynthetica 51:445–456.
- Long S, Zhu XG, Naidu S, Ort D (2006) Can improvement in photosynthesis increase crop yields? Plant Cell Environ 29: 315–330.

- McCree K (1972) The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agric For Meteorol 9: 191–216.
- Miao L, Zhang Y, Yang X, Xiao J, Zhang H, Zhang Z, Wang Y, Jiang G (2016) Colored light-quality selective plastic films affect anthocyanin content, enzyme activities, and the expression of flavonoid genes in strawberry (*Fragaria* × *ananassa*) fruit. Food Chem 207:93–100.
- Miao L, Zhang Y, Yang X, Xiao J, Zhang H, Jiang M, Zhang Z, Wang Y, Jiang G (2017) Fruit quality, antioxidant capacity, related genes, and enzyme activities in strawberry (*Fragaria* × ananassa) grown under colored plastic films. HortScience 52:1241–1250.
- Miao Y, Chen Q, Qu M, Gao L, Hou L (2019) Blue light alleviates 'red light syndrome' by regulating chloroplast ultrastructure, photosynthetic traits and nutrient accumulation in cucumber plants. Sci Hortic 257: 108680.
- Munekage Y, Hashimoto M, Miyake C, Tomizawa KI, Endo T, Tasaka M, Shikanai T (2004) Cyclic electron flow around photosystem I is essential for photosynthesis. Nature 429: 579–582.
- Murchie E, Horton P (1998) Contrasting patterns of photosynthetic acclimation to the light environment are dependent on the differential expression of the responses to altered irradiance and spectral quality. Plant Cell Environ 21: 139–148.
- Nawrocki WJ, Bailleul B, Picot D, Cardol P, Rappaport F, Wollman FA, Joliot P (2019) The mechanism of cyclic electron flow BBA Bioenergetics 1860: 433–438.
- Nishimura Y, Fukumoto Y, Aruga H, Shimoi Y (2009) Growth and developmental characteristics of vegetables grown under spectrum conversion film. Hortic Environ Biotechnol 50: 416–421.

- Nishimura Y, Wada E, Fukumoto Y, Aruga H, Shimoi Y (2012) The effect of spectrum conversion covering film on cucumber in soilless culture. Acta Hortic 956: 481–487.
- Novoplansky A, Sachs T, Cohen D, Bar R, Bodenheimer J, Reisfeld R (1990) Increasing plant productivity by changing the solar spectrum. Sol Energy Mater 21: 17–23.
- Ort D, Merchant S, Alric J, Barkan A, Blankenship R, Bock R, Croce R, Hanson M, Hibberd J, Long S, Moore T, Moroney J, Niyogi K, Parry M, Peralta-Yahya P, Prince R, Redding K, Spalding M, van Wijk K, Vermaas W, von Caemmerer S, Weber Andreas, Yeates T, Yuan J, Zhu XG (2015) Redesigning photosynthesis to sustainably meet global food and bioenergy demand. Proc Natl Acad Sci USA 112:8529–8536.
- Osmond C (1981) Photorespiration and photoinhibition. Some implications for the energetics of photosynthesis. BBA Bioenergetics 639: 77–98.
- Pan T, Ding J, Qin G, Wang Y, Xi L, Yang J, Li J, Zhang J, Zou Z (2019) Interaction of supplementary light and CO₂ enrichment improves growth, photosynthesis, yield, and quality of tomato in autumn through spring greenhouse production. HortScience 54: 246–252.
- Paradiso R, Meinen E, Snel J, De Visser P, Van Ieperen W, Hogewoning S, Marcelis LFM (2011) Spectral dependence of photosynthesis and light absorptance in single leaves and canopy in rose. Sci Hortic 127: 548–554.
- Park KS, Kwon JK, Lee DK, Son JE (2016) Microclimate and crop growth in the greenhouses covered with spectrum conversion films using different phosphor particle sizes. Protected Hort Plant Fac 25: 111–117.

- Pons T, De Jong-Van Berkel Y (2004) Species-specific variation in the importance of the spectral quality gradient in canopies as a signal for photosynthetic resource partitioning. Ann Bot 94: 725–732.
- Porra R, Thompson W, Kriedemann P (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.
- Sæbø A, Krekling T, Appelgren M (1995) Light quality affects photosynthesis and leaf anatomy of birch plantlets in vitro. Plant Cell Tissue Organ Cult 41: 177–185.
- Shengxin C, Chunxia L, Xuyang Y, Song C, Xuelei J, Xiaoying L, Zhigang X, Rongzhan G (2016) Morphological, photosynthetic, and physiological responses of rapeseed leaf to different combinations of red and blue lights at the rosette stage. Front Plant Sci 7:1144.
- Shikanai T (2014) Central role of cyclic electron transport around photosystem I in the regulation of photosynthesis. Curr Opin Biotechnol 26: 25–30.
- Shikanai T, Yamamoto H (2017) Contribution of Cyclic and Pseudo-cyclic Electron Transport to the Formation of Proton Motive Force in Chloroplasts. Mol Plant 10: 20–29.
- Shin J, Hwang I, Kim D, Moon T, Kim J, Kang WH, Son JE (2021) Evaluation of the light profile and carbon assimilation of tomato plants in greenhouses with respect to film diffuseness and regional solar radiation using raytracing simulation. Agric For Meteorol 296.

- Shiukhy S, Raeini-Sarjaz M, Chalavi V (2015) Colored plastic mulch microclimates affect strawberry fruit yield and quality. Int J Biometeorol 59: 1061–1066.
- Simkin A, López-Calcagno P, Raines C (2019) Feeding the world: Improving photosynthetic efficiency for sustainable crop production. J Exp Bot 70: 1119–1140.
- Sitko K, Rusinowski S, Pogrzeba M, Daszkowska-Golec A, Gieroń Ż, Kalaji, HM, Małkowski E (2020) Development and aging of photosynthetic apparatus of *vitis vinifera* L. during growing season. Photosynthetica 58: 186–193.
- Sood S, Gupta V, Tripathy B (2005) Photoregulation of the greening process of wheat seedlings grown in red light. Plant Mol Biol 59: 269–287.
- Splinter W (1974) Modelling of plant growth for yield prediction. Agric Meteorol 14: 243–253.
- Strasser AJ, Krüger GHJ, Strasser RJ, Van Heerden PDR (2006) Ranking of dark chilling tolerance in soybean genotypes probed by the chlorophyll a fluorescence transient O-J-I-P. Environ Exp Bot 56: 147–157.
- Takahashi S, Milward S, Fan D, Chow WS, Badger M (2009) How does cyclic electron flow alleviate photoinhibition in Arabidopsis? Plant Physiol 149: 1560–1567.
- Thornley JHM (1976) Mathematical models in plant physiology. Academic Press, London
- Trouwborst G, Hogewoning S, van Kooten O, Harbinson J, van Ieperen W (2016) Plasticity of photosynthesis after the "red light syndrome" in cucumber. Environ Exp Bot 121: 75–82.

- Tsimilli-Michael M, Strasser RJ (2008) Experimental resolution and theoretical complexity determine the amount of information extractable from the chlorophyll fluorescence transient OJIP. Photosynthesis. Energy from the sun: 697-701. Springer, Dordrecht.
- Tsimilli-Michael M (2019) Revisiting JIP-test: An educative review on concepts, assumptions, approximations, definitions and terminology. Photosynthetica 58: 275–292.
- Vasseur F, Pantin F, Vile D (2011) Changes in light intensity reveal a major role for carbon balance in Arabidopsis responses to high temperature. Plant Cell Environ 34: 1563–1576.
- Wang H, Gu M, Cui J, Shi K, Zhou Y, Yu J (2009) Effects of light quality on CO₂ assimilation, chlorophyll-fluorescence quenching, expression of Calvin genes and carbohydrate accumulation in Cucumis sativus. J Photoch Photobio B 96: 30–37.
- Wang J, Lu W, Tong Y, Yang Q (2016) Leaf morphology, photosynthetic performance, chlorophyll fluorescence, stomatal development of lettuce (*Lactuca sativa* L.) exposed to different ratios of red light to blue light. Front Plant Sci 7:1–10.
- Wang JH, Cai YF, Li SF, Zhang SB (2020). Photosynthetic acclimation of rhododendrons to light intensity in relation to leaf water-related traits. Plant Ecol 221: 407–420.
- Yamori W, Sakata N, Suzuki Y, Shikanai T, Makino A (2011) Cyclic electron flow around photosystem I via chloroplast NAD(P)H dehydrogenase (NDH) complex performs a significant physiological role during photosynthesis and plant growth at low temperature in rice. Plant J 68: 966– 976.

- Yamori W, Shikanai T, Makino A (2015) PhotosystemI cyclic electron flow via chloroplast NADH dehydrogenase-like complex performs a physiological role for photosynthesis at low light. Sci Rep 5: 13908.
- Yang X, Xu H, Shao L, Li T, Wang Y, Wang R (2018) Response of photosynthetic capacity of tomato leaves to different LED light wavelength. Environ Exp Bot 150: 161–171.
- Yoon HI, Kang JH, Kang WH, Son JE (2020a). Subtle changes in solar radiation under a green-to-red conversion film affect the photosynthetic performance and chlorophyll fluorescence of sweet pepper. Photosynthetica 58: 1107–1115.
- Yoon HI, Kim JH, Park KS, Namgoong JW, Hwang TG, Kim JP, Son JE (2020b) Quantitative methods for evaluating the conversion performance of spectrum conversion films and testing plant responses under simulated solar conditions. Hortic Environ Biotechnol 61: 999–1009.
- Yoshida Y, Sarmiento-Mañús R, Yamori W, Ponce MR, Micol JL, Tsukaya H (2018) The Arabidopsis *phyB-9* mutant has a second-site mutation in the *VENOSA4* gene that alters chloroplast size, photosynthetic traits, and leaf growth. Plant Physiol 178: 3–6.
- Zhang T, Maruhnich S, Folta, K (2011) Green light induces shade avoidance symptoms. Plant Physiol 157: 1528–1536.
- Zheng L, Van Labeke MC (2017) Long-term effects of red- and blue-light emitting diodes on leaf anatomy and photosynthetic efficiency of three ornamental pot plants. Front Plant Sci 8: 1–12.
- Zheng L, Van Labeke MC (2018) Effects of different irradiation levels of light quality on Chrysanthemum. Sci Hortic 233: 124–131.

- Zheng J, Ji F, He D, Niu G (2019) Effect of light intensity on rooting and growth of hydroponic strawberry runner plants in a LED plant factory. Agron J 9: 1–13.
- Zhu XG, De Sturler E, Long S (2007) Optimizing the distribution of resources between enzymes of carbon metabolism can dramatically increase photosynthetic rate: A numerical simulation using an evolutionary algorithm. Plant Physiol 145: 513–526.
- Zhu XG, Long S, Ort D (2008) What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? Curr Opin Biotechnol 19: 153–159.
- Zhu XG, Long S, Ort D (2010) Improving photosynthetic efficiency for greater yield. Annu Rev Plant Biol 61: 235–261.

ABSTRACT IN KOREAN

기능성 필름은 온실 내 작물 생장을 위한 광환경을 증진시키기 위해 도입되어왔다. 이러한 필름 중, 입사된 태양광 중 녹색광을 적색광으로 전환시키는 광전환필름은 다양한 작물의 생산량을 증가시키는 것으로 알려져 있다. 하지만 이 결과는 항상 일정하지 않고 작물 생장이 증가되는 원인 또한 완전히 밝혀지지 않았다. 본 연구는 적색 광전화필름의 누적 효과가 딸기 작물의 전자전달과 광합성 능력에 미치는 영향을 규명하고자 하였다. 이를 위해 폴리에틸렌 필름과 광전환필름 하에서 자란 딸기의 광합성 효율, 엽광학적 특성, 엽록소 함량, 엽록소 형광, 생육 및 과실 품질이 평가되었다. 광전환필름에 의해 변형된 태양광은 엽광학적 특징과 엽록소 함량을 변화시키지 않았지만 광계 [전자 수용체의 화원과 전자전달의 효율에 관련된 엽록소 형광 지표들을 유의하게 증가시켰다. 광전환필름 하에서 재배된 딸기는 비광화학적 소산의 증가없이 광계 [. 광계 [] 의 전자전달량과 순화적 전자전달량이 폴레에틸렌 필름에서 자란 딸기보다 유의하게 높았다. 정식 후 48 일 이후부터는 단일엽 및 전체 식물체의 광합성 효율 또한 광전환필름 처리구가 대조구보다 유의하게 증가되었다. 영양 생장은

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광전환필름에 의해 영향을 받지 않았지만 딸기 과실의 평균 과실중량, 당도, 산도, 경도는 광전환필름 처리구에서 유의하게 증진되었다. 이러한 결과는 광전환필름에 의해 변형된 태양광은 광저해현상 없이 전자전달을 증가시켜 광합성 능력과 과실의 질을 증진시켰음을 나타낸다.

주요어: 광스펙트럼, 광화학반응계, 딸기, 엽록소 형광, JIP 분석

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