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Subtle changes in solar radiation under a green-to-red conversion film affect the photosynthetic performance and chlorophyll fluorescence of sweet pepper

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Abstract

Although spectrum conversion films are used to improve the photosynthetic efficiency and, ultimately, crop growth, the effects of the modified spectrum on photosynthetic traits in plants have not yet been sufficiently reported. The objective of this study was to investigate the changes in photosynthetic performance and chlorophyll fluorescence of sweet pepper (*Capsicum annuum* L.) under a green-to-red conversion (GtR) film. The GtR-modified spectrum increased the dry mass and decreased the petiole length. The photosynthetic light-response curves were significantly improved, and the gap of the maximum photosynthetic rates increased over time after covering. The GtR-modified spectrum significantly increased chlorophyll fluorescence parameters in the JIP-test, such as parameters related to the reduction of end electron acceptors on the PSI acceptor side, the efficiency for electron transport in PSII, and the performance indexes. Our data indicated that the GtR-modified spectrum promotes electron transfer around PSI, improving photosynthetic performance and growth.

Additional key words: bell pepper; chlorophyll fluorescence transient; gas exchange; light adaptation; light quality.

Introduction

The research on the effects of light quality on plants has mostly focused on growth and morphology (Smith 1982, Patil *et al.* 2001, Li *et al.* 2003, Niinemets 2010, Stanton *et al.* 2010, Dieleman *et al.* 2019). Recently, research focusing on photosynthetic capacity according to light quality using artificial irradiance has been reported in detail. Different monochromatic lights, such as blue and red, affected not only growth and morphology but also chlorophyll (Chl) contents, stomatal conductance, and net photosynthetic rate (Lee *et al.* 2007). The different light qualities may alter the activity of the photosynthetic apparatus in leaves and the expression of the Calvin cycle enzymes, inducing changes in photosynthetic capacity (Wang *et al.* 2009). In addition, the effect of light quality on photosynthetic response could be interpreted by photosynthetic electron transport of PSII and PSI, cyclic electron flow (CEF), and other Chl fluorescence parameters (Yang *et al.* 2018). Plants perform different photosynthetic acclimation reactions depending on short- or long-term changes in light quality (Dietzel *et al.* 2008).

Greenhouse coverings, such as films, modify solar radiation coming into the greenhouse to create a light environment for plants. Spectrum conversion film (SCF) is a functional covering film that is used to improve the light spectrum for plant growth and photosynthesis (Lamnatou and Chemisana 2013). SCF converts low-efficiency wavelengths into high-efficiency wavelengths, such as ultraviolet to blue and green to red, based on spectral quantum yield for carbon fixation (McCree 1971, Paradiso *et al.* 2011). The film was called a green-to-red 'conversion' film, but to be precise, it absorbs green lights and emits red lights. Many research studies have shown the remarkable effects of SCF on yields in various crops, such as tomato, strawberry, radish, cucumber, and lettuce (Novoplansky *et al.* 1990, Hemming *et al.* 2006, Hidaka *et al.* 2008, Nishimura *et al.* 2012, Kwon *et al.* 2013, Park *et al.* 2016). Although SCFs have been developed to improve photosynthetic efficiency, the effects of the

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Abbreviations: ABS/CS – absorption flux (exciting PSII antenna pigments) per exited cross-section; Area – complementary area above the fluorescence curve; CEF – cyclic electron flow; Chl – chlorophyll; DAC – days after covering; DI_0/CS – dissipated energy flux per exited cross-section; ET_0/CS – electron transport flux per exited cross-section; M_0 – the initial slope of the fluorescence transient normalized on the maximal variable fluorescence; PI_{ABS} – performance index on absorption basis; PI_{total} – total performance index; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; R_D – respiration rate; RE_0/CS – energy flux reducing end electron acceptors at the PSI acceptor side, per exited cross-section; TR/CS – trapped energy flux (leading to Q_A reduction) per exited cross-section; δ_{Ro} – probability with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side (RE); θ – photosynthetic quantum yield at zero irradiance; φ_{Eo} – quantum yield for electron transport (ET); φ_{Po} – maximum quantum yield for primary photochemistry; φ_{Ro} – quantum yield for reduction of end electron acceptors at the PSI acceptor side (RE); ψ_{Eo} –probability with which an electron moves further than Q_A^-.

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modified spectrum on photosynthetic traits in plants have not been fully reported.

Natural light is not monochromatic light but a spectrum of many different wavelengths that simultaneously affect plants. Subtle spectral changes in incident solar radiation, *i.e.*, SCF-transmitted spectra, could not be interpreted solely according to previous research using monochromatic lights. Li *et al*. (2017) suggested that increasing CEF around PSI in *Arabidopsis* is one of the mechanisms by which SCF promotes CO_2 fixation. A few research studies related to photosynthetic response under altered natural light were conducted using colored shade nets (Oliveira *et al.* 2016, Tafoya *et al.* 2018). Modified natural light environments, such as with photoselective film and screenhouses, affected the growth and photosynthetic acclimation of sweet pepper (*Capsicum annuum* L.), but the effect under SCF has not been reported yet (Li *et al.* 2000, Kong *et al.* 2013, Kitta *et al.* 2014a,b).

We wondered if the increase in photosynthetic efficiency through the SCF would actually lead to an increase in growth and, if so, how and when photosynthetic traits would change. Thus, the objective of this study was to investigate the SCF-induced effects on the growth, morphology, and photosynthetic performance through Chl fluorescence transient and gas-exchange parameters in sweet peppers.

Materials and methods

Plant material and growth conditions: Sweet pepper seedlings (*Capsicum annuum* L. cv Kori) were grown in a commercial nursery for 45 d and then transferred to a Venlo-type glass greenhouse at the experimental farm of Seoul National University, located in Suwon, Korea (37°16'N, 126°59'E). The air temperature was set at 25/15°C day/night with roof vents and hot-water pipe systems. On 30 August 2019, the seedlings were transplanted into pots filled with commercial soils for horticultural crops (*Baroker*, *Seoul Bio Co.*, *Ltd.*, Eumseong, Korea). After transplanting, PBG nutrient solution from the Netherlands was applied with an electrical conductivity of 0.6 dS m^{-1} (de Kreij *et al.* 1999). At 32 d after transplanting, the pots were transferred to a small-sized greenhouse [2.0 (length) × 3.0 (width) × 2.0 m (height)] covered with experimental films, in which the upper leaves of plants were exposed to irradiance at a maximum intensity of 500 W m^{-2} [approximately 2,300 μmol(photon) m^{-2} s^{-1}] on sunny days. Four plants per treatment were harvested at 44 d after covering (DAC).

Film treatment and spectral characteristics: Experimental films used to cover the greenhouse included a commercial polyethylene (C-PE) film (*Tajopyo PE*, *Taekwangnewtec Co.*, *Ltd.*, Seoul, Korea) as the control and a spectrum conversion film, which converts green lights to red lights (GtR film), for the treatment condition. Light spectra under the C-PE and GtR films were measured using a spectroradiometer (*BLUE-Wave* spectrometer, *StellarNet*, *Inc.*, Tampa, FL, USA) at the experimental site at 13:00 h on 6 October 2019. The total transmittance (sum of specular and diffuse transmittances) of the films was measured at room temperature using the spectroradiometer connected to an integrating sphere (*IC-2*, *StellarNet*, *Inc.*) in the range of 300 to 900 nm. A solar simulator (*XIL-01B50KPV1*, *SERIC*, *Ltd.*, Tokyo, Japan) was used as the light source. The transmittance was measured before covering and after harvest.

Growth and morphological parameters: As an early growth indicator, plant height, stem diameter, and the numbers of nodes and leaves were measured with six replicates at 5, 13, and 19 DAC. Growth and morphological parameters, including leaf length and width, petiole length, internode length, the number of leaves and nodes, and the fresh mass of leaves, stems, and fruits were measured with three plants at harvest (44 DAC). The internode length was calculated by dividing the total length of internodes by the number of nodes. Additionally, the SPAD value was measured using a Chl meter (*SPAD-502*, *Konica Minolta*, Tokyo, Japan) five times per replicate. The dry mass of leaves, stems, and fruits was measured after drying in an even at 70°C for 72 h. The leaf area per plant was calculated using *ImageJ 1.49* image analysis software (*National Institutes of Health*, Bethesda, MD, USA).

Gas-exchange measurement: Photosynthetic rates were measured using a portable photosynthetic system (*LI-6400XT*, *Li-cor*, Lincoln, NE, USA) and an LED light source (*6400-02B*, *Li-cor*). The fourth leaf from the top of the plant was used to measure the photosynthetic light curve with four replicates at 5, 13, and 44 DAC. Before all measurements, the leaves were adapted under the light source (approximately 15 min) at a PPFD of 1,000 μmol(photon) m^{-2} s^{-1}. The conditions in the leaf chamber were kept constant (leaf temperature was 26.1 ± 0.62°C, relative humidity was 58.6 ± 1.3%, and CO_2 concentration was 400 ppm). The measurements were taken at irradiance levels of 2,000; 1,500; 1,200; 900, 600, 400, 200, 100, 50, and 0 μmol(photon) m^{-2} s^{-1} PPFD. Light-response curves for CO_2 assimilation were fitted to a rectangular hyperbola Michaelis-Menten-based model according to previous studies (Thornley 1976, Givnish 1988, Lobo *et al.* 2013):

$$P_{\mathrm{N}} = -R_{\mathrm{D}} + \frac{P_{\mathrm{Nmax}} \times I}{P_{\mathrm{Nmax}}/\theta + I} \tag{1}$$

where P_N is the net photosynthetic rate [μmol m^{-2} s^{-1}], R_D is dark respiration rate [μmol m^{-2} s^{-1}], P_{Nmax} is the maximum net photosynthetic rate [μmol m^{-2} s^{-1}], I is the photosynthetic photon flux density [μmol(photon) m^{-2} s^{-1}], and θ is the quantum yield at $I = 0$ μmol(photon) m^{-2} s^{-1}.

Chl fluorescence transient: The Chl fluorescence transient was measured on intact leaves using a Chl fluorescence meter (*Handy PEA*, *Hansatech*, King's Lynn, UK) at 49 DAC. The middle part of the first fully expanded leaf was dark-adapted for 20 min using a leaf clip (*HPEA/LC*, *Hansatech*), with 16 replicates per treatment. Fast fluorescence transients were taken using a saturating pulse of

1,500 μmol(photon) m^{-2} s^{-1}, a pulse duration of 1 s, and a fixed gain of 1×. The Chl fluorescence kinetic parameters were obtained based on the theory of energy flow in PSII and using the JIP-test according to previous studies (Strasser *et al.* 2000, Rapacz 2007, Kosmala *et al.* 2012, Gururani *et al.* 2015, Stirbet *et al*. 2018, Yoon *et al.* 2020), as described in Appendix.

Statistical analysis: For all measurements, the means of the C-PE and GtR films were compared *via Student*'s *t*-test with each replicate (P<0.1, 0.05, and 0.01). *R* software (*R 3.6.2*, *R Foundation*, Vienna, Austria) was used for the statistical analysis containing the regression analysis of the light-response curve for photosynthesis.

Results

Spectral characteristics: The spectral distributions of solar radiation in a greenhouse covered with the C-PE and GtR films are shown in Fig. 1. The photon flux transmitted through the GtR film increased by 7% at the red wavelengths of 600–700 nm, increased by 5.2% at the far-red wavelengths of 700–800 nm, and decreased by 1.9% at the blue-green wavelengths of 400–600 nm compared to the C-PE film. The red and far-red (R:FR) ratios under the C-PE and GtR films were 1.27 and 1.29, respectively (1.31 without cover). The total transmittance of the GtR film increased by 3.4% at the red wavelengths and decreased by 0.6–0.7% at the blue-green wavelengths compared to the C-PE film (Fig. 2*C*, Table 1). The transmittance higher than 100% at the red wavelength was caused by GtR film, which means that the transmitted light was greater than the incident light. The transmittance of the films measured 49 d after covering decreased in all wavelength ranges compared to the situation before covering. The transmittance differences in the C-PE film before and after covering were greater than those of the GtR film, especially in the range of 600–750 nm.

Plant growth and morphology: The initial growth and morphology, such as the plant height, the number of nodes and leaves, in the sweet peppers grown under the GtR film were significantly higher than those under the C-PE film (Fig. 2). The plants under the GtR film were significantly taller by 6.2–7.6% at 5–19 DAC than those under the C-PE film. The height at 44 DAC was similar in the C-PE and GtR film treatments (data not shown). The stem diameters of the plants under the C-PE and GtR films were not significantly different. The numbers of nodes in the plants under the GtR film significantly increased by 12.3 and 5.9% at 5 and 13 DAC, respectively, compared to those under the C-PE film, but were not significantly different at 19 and 44 DAC (Fig. 2*C*, Table 2). The number of leaves under the GtR film was significantly higher than that under the C-PE film by 7.2% at 13 DAC, but was not significantly different in other measurement periods. At 44 DAC, the total dry mass (sum of the leaves, stems, and fruits) of the plants grown under the GtR film significantly increased by 19.1% compared to that under the C-PE film (Table 2). The petiole length of the plants under the GtR film significantly

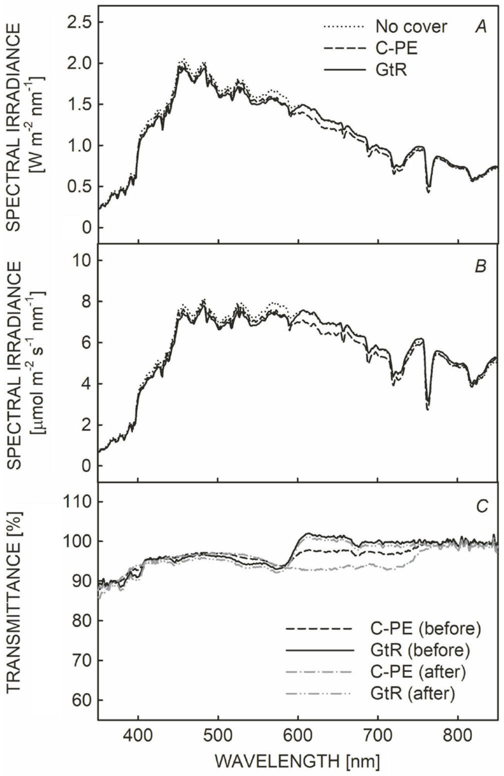

Fig. 1. Spectroscopic characteristics of the C-PE and GtR films. The spectral distributions of incident light under the films (*A*,*B*) were measured in the experimental site at 13:00 h on 6 October 2019. The total transmittances (*C*) were measured before and 49 d after covering using a spectroradiometer with an integrating sphere. The total transmittance (sum of specular and diffuse transmittances) was expressed as a percentage of incident light as 100%.

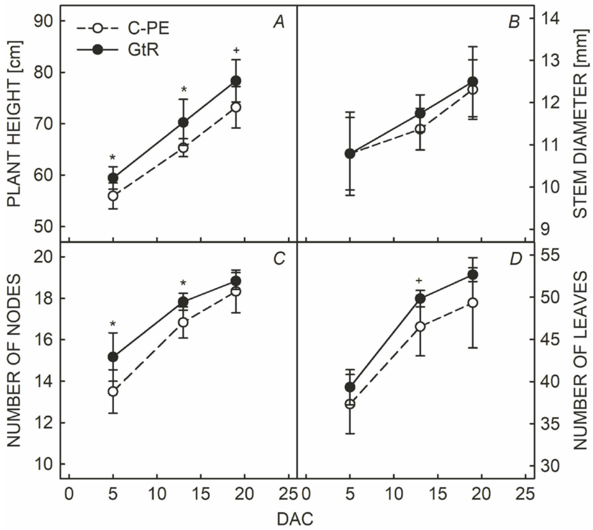

Fig. 2. Plant height (*A*), stem diameter (*B*), and the numbers of nodes (*C*) and leaves (*D*) of sweet pepper grown under the C-PE and GtR films at 5, 13, and 19 d after covering (DAC). The vertical bars indicate SD, n = 6. The symbols indicate significant differences (*Student*'s *t*-test, ^{+}P<0.1, $^{*}P$<0.05).

Table 1. Spectral transmittance [%] of the C-PE and GtR films before and 49 d after covering.

Spectrum	Range [nm]	Before		After (49 d)	
		C-PE	GtR	C-PE	GtR
Ultraviolet	300–400	89.4	90.0	88.0	89.1
Blue	400–500	96.1	95.6	95.9	94.7
Green	500–600	95.5	94.8	95.4	94.0
Red	600–700	97.3	100.0	93.3	99.8
PAR	400–700	96.3	97.0	94.9	96.2
Far-red	700–800	98.4	99.8	96.2	98.9

Table 2. Growth and morphology of the sweet peppers grown under the C-PE and GtR films at 44 d after covering. Data are presented as mean ± SD (n = 3). The plus (+) indicates a significant difference at P<0.1 (*Student*'s t-test). ns – not significant.

Parameter		C-PE	GtR	
Fresh mass [g]	Leaf	234.7 ± 1.2	245.3 ± 30.1	ns
	Stem	137.3 ± 3.1	152.0 ± 19.1	ns
	Fruit	921.3 ± 199.0	1,157.3 ± 74.5	ns
	Total	1,293.3 ± 198.0	1,554.7 ± 106.0	ns
Dry mass [g]	Leaf	25.4 ± 1.6	28.1 ± 3.5	ns
	Stem	17.5 ± 0.6	19.1 ± 2.3	ns
	Fruit	47.2 ± 10.1	60.1 ± 2.7	ns
	Total	90.1 ± 12.2	107.3 ± 6.2	+
Total number	Leaf	52 ± 5	59 ± 4	ns
	Fruit	10 ± 2	11 ± 1	ns
Internode length [nm]		4.5 ± 0.3	4.6 ± 0.4	ns
Leaf length [cm]		21.2 ± 0.5	21.7 ± 0.9	ns
Leaf width [cm]		11.9 ± 0.3	12.3 ± 1.2	ns
Petiole length [cm]		11 ± 0.4	9.8 ± 0.7	+
Leaf area [cm^2]		5,323.0 ± 246.9	5,661.1 ± 698.1	ns

decreased by 10.2% compared to that under the C-PE film. The dry mass of fruits in the plants under the GtR film was 27.3% heavier than that under the C-PE film but not significantly different. The other parameters measured at harvest were not significantly different in the C-PE and GtR treatments. The SPAD values of leaves under the GtR film were 6.4% higher at 19 DAC and 3.6% higher at 44 DAC than those under the C-PE film, but not significantly different (data not shown).

Photosynthetic light response: The difference in the net photosynthetic rate (P_N) for the sweet pepper leaves grown under the C-PE and GtR films was significantly and steadily greater over the days after covering (Fig. 3). At 5, 13, and 44 DAC, the parameters of the light-response curves are shown in Table 3. The maximum photosynthetic rates (P_{Nmax}) under the GtR film increased by 2.0, 29.1, and 42.5% at 5, 13, and 44 DAC, respectively, compared to those under the C-PE film. The dark respiration (R_D) and quantum yield at zero irradiation (θ) under the GtR film increased at 5 DAC but decreased at 44 DAC

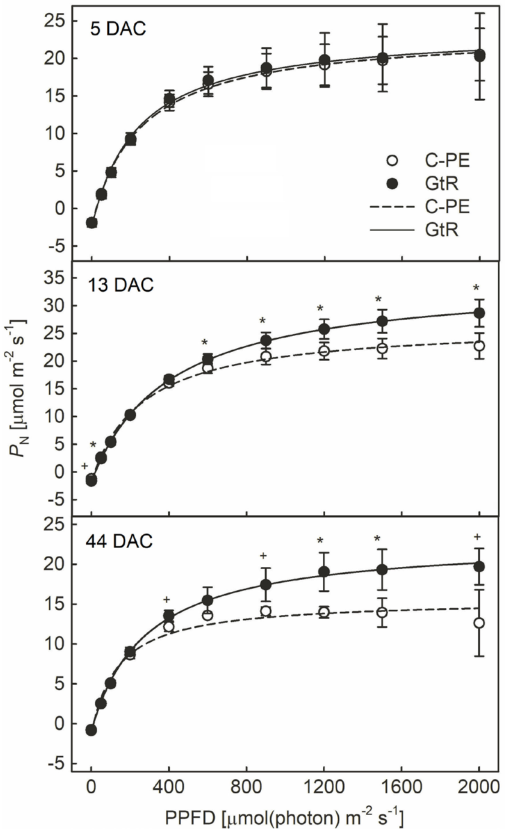

Fig. 3. Light-response curves of net photosynthesis (P_N) in the first fully expanded leaves of sweet pepper grown under the C-PE and GtR films at 5, 13, and 44 d after covering (DAC). The regression curves were obtained by Eq. 1, and the parameters refer to Table 3. The vertical bars indicate SD, n = 3–4. The symbols indicate significant differences (*Student*'s t-test, ^+P<0.1, $^*P$<0.05).

Table 3. The parameters (R_D, P_{Nmax}, and θ) and coefficient of determination (R^2) for photosynthetic light-response curves of the sweet peppers grown under the C-PE and GtR films at 5, 13, and 44 d after covering (DAC). P_{Nmax} – light-saturated net photosynthetic rate; R_D – respiration rate; θ – photosynthetic quantum yield at zero irradiance.

DAC	Film	R_D [µmol m^{-2} s^{-1}]	P_{Nmax} [µmol m^{-2} s^{-1}]	θ	R^2
5	C-PE	2.159	25.804	0.104	0.956
	GtR	2.425	26.315	0.111	0.919
13	C-PE	1.721	28.422	0.110	0.982
	GtR	1.748	36.685	0.091	0.988
44	C-PE	1.360	16.910	0.124	0.922
	GtR	0.995	24.101	0.087	0.967

compared to those under the C-PE film. The coefficient of determination (R^2) was very high and ranged from 0.919 to 0.988, meaning that the rectangular hyperbola equation (Eq. 1) performed well to fit the light-response curves.

Chl fluorescence transient: The Chl fluorescence transient parameters of the sweet pepper leaves grown under the C-PE and GtR films showed the spectrum-induced effects on PSII and PSI (Fig. 4). The parameters, such as the area between the fluorescence induction curve and the maximal fluorescence intensity (Area), the phenomenological energy flux reducing end electron acceptors at the PSI acceptor side per excited cross section (RE_0/CS), the probability to move an electron further than Q_A^- (ψ_{Eo}), the quantum yield for electron transport (φ_{Eo}), the probability that an electron is transported from reduced plastoquinone (PQ) to the electron acceptor side of PSI (δ_{Ro}), the quantum yield for reduction of end electron acceptors at the PSI acceptor side (φ_{Ro}), and 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}), significantly increased under the GtR film compared to the C-PE film. The normalized initial slope (in ms^{-1}) of the fluorescence transient (M_0) significantly decreased under GtR film compared to the C-PE film. The phenomenological energy fluxes absorbed by antenna pigments (ABS/CS), dissipated (DI_0/CS), trapped in PSII reaction centers (TR/CS), and used for electron transport (ET_0/CS) per excited cross-section, and the maximum quantum yield for primary photochemistry (φ_{Po}) under the C-PE and GtR films were quite similar. The specific energy fluxes (per Q_A-reducing PSII reaction center), *i.e.*, ABS/RC, DI_0/RC, TR/RC, ET_0/RC, and RE_0/RC, of leaves grown under the C-PE and GtR films were consistent with the results of each phenomenological flux parameter (data not shown).

Discussion

We evaluated the cumulative effects of the modified solar spectrum on growth, morphology, the photosynthetic light response, and Chl fluorescence transient in sweet peppers grown under a spectrum conversion film. This photoluminescence property is commonly measured using a spectrofluorometer (Pogreb *et al.* 2004, Wondraczek *et al.* 2013, El-Bashir *et al.* 2016, Qi *et al.* 2016). In this study, the spectral properties of the GtR film were evaluated at the experimental site and according to the total transmittance (Fig. 1). The transmitted spectra showed the modified spectrum actually reaching the crops, which is a general method for evaluating the properties of greenhouse covering materials (De Salvador *et al.* 2008, Kwon *et al.* 2017). Due to the luminescent properties of GtR film emitting red light in all directions, the total transmittance was measured using an integrating sphere (Schettini and Vox 2010). The photoluminescent effect of GtR film in the spectrum under solar radiation was less visible than that in the transmittance under the artificial lighting, which was consistent with other photoluminescent films (Schettini *et al.* 2011). The indoor measurements of total transmittance showed that the properties of the GtR film had changed less than 2% on day 44 after covering (Table 1, Fig. 1*C*). The decreases in transmittance of red wavelengths indicate decreases in red emission, which are caused by photodegradation of the fluorescent dye molecules (El-Bashir *et al.* 2016). The long-term photostability of the film is an important obstacle for its use as a greenhouse cover but it did not have a large effect during the experiment described in this study.

The subtle changes in the solar spectrum could affect the growth and morphology of the sweet peppers grown under the GtR film. Although the initial effect of GtR on morphology was not maintained until harvest, the total dry mass significantly increased under the GtR film (Fig. 2, Table 2). Similarly, green-to-red SCFs improved the mass and yield in various crops, such as tomato, cucumber, and lettuce (Novoplansky *et al.* 1990, Nishimura *et al.* 2012, Park *et al.* 2016). In this study, the petiole length decreased under the GtR film, with a higher R:FR ratio than that of the C-PE film (Table 2). The extension of petiole growth is a phytochrome-regulated response, allowing the leaves to be placed in a light environment against the shade environment where R:FR ratio is low (Lötscher and Nösberger 1997, Ranwala *et al.* 2002). Since plants can increase the petiole length to improve light interception (Takenaka 1994, Duursma *et al.* 2012), it is possible that the diffuse light increased by the red light emission of the GtR film suppressed this elongation.

The cumulative effects of a modified spectrum on photosynthetic capacity could be evaluated as photosynthetic light response using the same LED light source. In this study, the difference in the light-response curves under the GtR and C-PE films did not appear on 5 DAC, occurred on 13 DAC, and remained until 44 DAC (at harvest), meaning that the cumulative effects improved the photosynthetic capacity in 1–2 weeks (Fig. 3). Similarly, Li *et al.* (2017) showed that the net photosynthetic rate in *Arabidopsis* grown under SCF significantly increased at PPFD of 1,200 μmol(photon) m^{-2} s^{-1} compared to the control. McCree (1971) reported that the spectral quantum yields for CO_2 uptake were higher and had two maxima

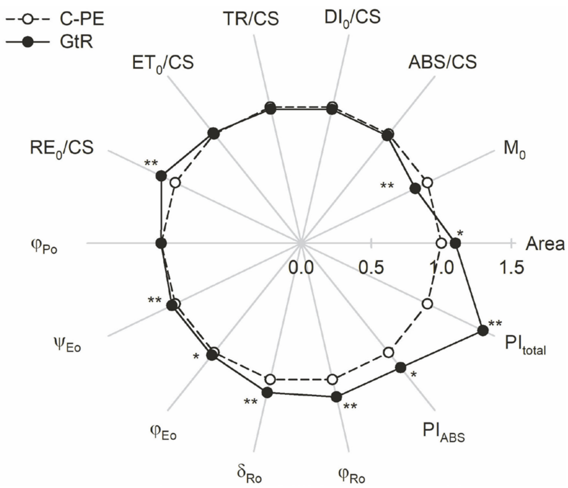

Fig. 4. Chlorophyll fluorescence parameters derived from JIP-test analyses in the first fully expanded leaves of sweet peppers grown under the C-PE and GtR films at 49 d after covering with 16 replicates. Each parameter was normalized on that of the C-PE in the plot and is described in the text. The asterisks indicate significant differences (*Student*'s *t*-test, $^*P<0.05$, $^{**}P<0.01$).

in the red and blue wavelengths, which is consistent with other research (Inada 1976, Paradiso *et al.* 2011). The increases in photosynthesis under the GtR film may be driven by the higher quantum yield of red light. However, this interpretation could not explain the results of measurements using the same LED light source, and it did not include the effects of photosynthetic acclimation. The long-term adaptation of plants to a specific environment over several days results from protein and pigment synthesis (Dau 1994). The plants subjected to a stable light quality gradient perceive the imbalanced photosystem excitation and respond by state transitions as a short-term response or readjustment of photosystem stoichiometry as a long-term response (Dietzel *et al.* 2008). Unfortunately, our findings were not sufficient to interpret these observations in detail, and further research is needed. The photosynthesis results were numerically compared with the parameters (R_D, P_{Nmax}, and θ) of the photosynthetic model in Eq. 1 (Table 3). The rectangular hyperbola model is a simple model that describes the photosynthetic light-response curve (Chen *et al.* 2011, Lobo *et al.* 2013).

Furthermore, the modified spectrum affects the Chl fluorescence transient in sweet peppers grown under the GtR film, and its effects are only shown in particular parameters of the JIP-test (Fig. 4). The JIP-test, used to interpret the fluorescence signals into the phenomenology and biophysics of the photosynthetic apparatus, allows quantification of the functional photosynthetic properties and a detailed evaluation of the impact of the physiological state changes caused by separate treatments (Strasser *et al.* 2000, 2004; Tsimilli-Michael and Strasser 2008). The performance index, PI_{ABS}, is a multiparametric expression of three functional steps, *i.e.*, light energy absorption (ABS), excitation energy trapping (TR), and conversion of excitation energy to electron transport (ET), which contribute to overall photosynthesis. The PI_{ABS} is known as a sensitive parameter regardless of the type of plant and abiotic stress (Strauss *et al.* 2006, Živčák *et al.* 2008, Bussotti *et al.* 2010, Kalaji *et al.* 2012, Ceusters *et al.* 2019). Although the energy fluxes for PI_{ABS}-related parameters, *i.e.*, ABS/CS, TR/CS, ET/CS, and φ_{Po} (= TR_0/ABS), were unchanged, the PI_{ABS} significantly increased under the GtR film due to increases in ψ_{Eo} and φ_{Eo} (Fig. 4). The term Eo is related to electron transport from Q_A^- to the intersystem electron acceptors, *i.e.*, Q_B, PQ pool, cytochrome b_6f, and plastocyanin. That is, the GtR-promoted photosynthetic efficiency in PSII was influenced by the electron transfer efficiency rather than the quantum yield of primary photochemistry (φ_{Po}, called as F_v/F_m). Similarly, the commonly used φ_{Po} in various abiotic stresses is highly insensitive, while the PI_{ABS} is more sensitive (Tsimilli-Michael and Strasser 2008, Živčák *et al.* 2008, Yoon *et al.* 2020). The normalized initial slope, M_0, expresses the net rate of electron trapping, increasing the number of closed reaction centers, and can be decreased by electron transport from Q_A to Q_B (Strasser *et al.* 2004, Stirbet and Govindjee 2011).

The terms RE and Ro represent the reduction of end acceptors at the PSI electron acceptor side, such as NADP and ferredoxin (Fd), and have been discussed recently (Tsimilli-Michael and Strasser 2008, Stirbet and Govindjee 2011, Stirbet *et al.* 2018). The total performance index, PI_{total}, is an extended parameter of PI_{ABS} and incorporates the performance up to the PSI end electron acceptors (RE); thus, it is the most sensitive parameter and expresses the overall potential for energy conservation (Yusuf *et al.* 2010, Gururani *et al.* 2015). In this study, the modified spectrum under the GtR film induced significant increases in all RE-related parameters, such as RE_0/CS, δ_{Ro}, φ_{Ro}, and PI_{total} (Fig. 4). We can therefore deduce that the photosynthetic performance around the PSI electron acceptor side was enhanced and resulted from the increased energy flux, efficiency, and quantum yield for the reduction of end acceptors at the PSI side, such as NADP and Fd. Light quality could dynamically affect the CEF around PSI by state transition and photosystem stoichiometry readjustments, including the thylakoid membrane system (Wollman 2001, Allen 2003, Dietzel *et al.* 2008). Li *et al.* (2017) proposed that alteration to the spectrum by SCF could lead to variations in electron flow and increased CEF around PSI. The authors showed that the Fd-dependent PQ reduction level increased in WT *Arabidopsis* grown under SCF, whereas the increases did not appear in mutant *pgr5*, which lacks functions of the PROTON GRADIENT REGULATION 5 protein and is defective in Fd-dependent CEF, regardless of the film used. In addition, their results are in line with ours, which indicate the increased efficiency for electron transfer (ψ_{Eo} and φ_{Eo}) and the increased PQ pool reduction (Area) here (Fig. 4). If so, the increased CEF by the SCF-modified spectrum could improve the electron transport capacity and RE capacity, accelerating CO_2 fixation.

This study compared the growth, morphology, and photosynthesis of sweet peppers over time after covering with a green-to-red conversion film and investigated the photosynthetic responses through Chl fluorescence transient and gas-exchange parameters in detail. The solar radiation with red light emission by the GtR film induced photosynthetic acclimation, affecting the growth and morphology of the plants. The photosynthetic light-response curves and P_{Nmax} showed that the cumulative effects of the GtR-modified spectrum improved the photosynthetic capacity after only two weeks. In the Chl fluorescence transient, the spectrum increased the efficiency of electron transfer up to intersystem electron acceptors (ψ_{Eo}, φ_{Eo}). The parameters related to the reduction of end acceptors at the PSI electron acceptor side (RE_0/CS, δ_{Ro}, φ_{Ro}, and PI_{total}) were mostly changed, and the photosynthetic capacities were promoted under the GtR film. We concluded that the subtle changes in solar radiation modified by the GtR film could promote the electron transfer around PSI, improving the photosynthetic capacity and plant growth.

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Appendix. Formulae and glossary of terms used by the JIP-test in the study (modified after Strasser *et al.* 2004).

Data extracted from the recorded fluorescence transient OJIP	
F_t	fluorescence at time t after the onset of actinic illumination
$F_0 = F_{50\mu s}$	minimal fluorescence intensity (50 µs)
$F_{300\mu s}$	fluorescence intensity at 300 µs
$F_J = F_{2ms}$	fluorescence intensity at the J-step (2 ms) of OJIP
$F_I = F_{30ms}$	fluorescence intensity at the I-step (30 ms) of OJIP
$F_M = F_P$	maximal fluorescence intensity, at the peak P of OJIP
Area	total complementary area between the fluorescence induction curve and F_M
Fluorescence parameters derived from the extracted data	
$F_V = F_M - F_0$	maximal variable fluorescence
$V_t = (F_t - F_0)/F_V$	relative variable fluorescence
$M_0 = (\Delta V/\Delta t)_0 \approx 4 \times [(F_{300\mu s} - F_{50\mu s})/(F_M - F_{50\mu s})]$	initial slope (in ms^{-1}) of the O–J fluorescence rise

Specific energy fluxes (per Q_A-reducing PSII reaction center – RC)	
$ABS/RC = (M_0/V_J)/\varphi_{Po}$	absorption flux (exciting PSII antenna pigments) per RC
$TR_0/RC = M_0/V_J$	trapping flux (leading to Q_A reduction) per RC
$ET_0/RC = (M_0/V_J) \times \psi_{Eo}$	electron transport flux (from Q_A^- to PQ) per RC
$DI_0/RC = (ABS/RC) - (TR_0/RC)$	dissipated energy flux per RC (at t = 0)
$RE_0/RC = (M_0/V_J) \times (1 - V_I)$	electron transport flux (from Q_A^- to final PSI acceptors) per RC
Quantum yields and efficiencies	
$\psi_{Eo} = ET_0/TR_0 = 1 - V_J$	probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A^-
$\psi_{Ro} = RE_0/TR_0 = 1 - V_I$	probability that a trapped exciton moves an electron into final PSI acceptors
$\delta_{Ro} = RE_0/ET_0 = \psi_{Ro}/\psi_{Eo}$	efficiency with which an electron from the intersystem electron carriers moves to reduce final PSI acceptors
$\varphi_{Po} = TR_0/ABS = F_V/F_M$	maximum quantum yield of primary PSII photochemistry
$\varphi_{Ro} = RE_0/ABS = \varphi_{Po}/(1 - V_I)$	quantum yield for reduction of end electron acceptors at the PSI acceptor side
$\varphi_{Eo} = ET_0/ABS = \varphi_{Po}/(1 - V_J)$	quantum yield of electron transport (at t = 0)
Phenomenological fluxes	
$ABS/CS = (M_0/V_J)/\varphi_{Po}$	absorption flux per excited cross section of PSII
$TR/CS = (TR_0/ABS) \times (ABS/CS)$	trapping flux per excited cross section of PSII
$ET_0/CS = (ET_0/ABS) \times (ABS/CS)$	electron transport flux per excited cross section of PSII
$DI_0/CS = (DI_0/ABS) \times (ABS/CS)$	dissipated energy flux per excited cross section of PSII
$RE_0/CS = (RE_0/ABS) \times (ABS/CS)$	electron flux reducing end electron acceptors at the PSI acceptor side per excited cross section of PSII
Performance indexes	
$PI_{ABS} = (RC/ABS) \times [\varphi_{Po}/(1 - \varphi_{Po})] \times [\psi_{Eo}/(1 - \psi_{Eo})]$	performance index on absorption basis
$PI_{total} = PI_{ABS} \times [\delta_{Ro}/(1 - \delta_{Ro})]$	total performance index on absorption basis