A THESIS FOR THE DEGREE OF MASTER OF SCIENCE

Evaluation of light use efficiency and water use efficiency of sweet peppers subjected to LED inter-lighting in greenhouses

온실 내 군락 내부 LED 보광에 의한 파프리카의 광 이용 효율 및 물 이용 효율 평가

BY

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AUGUST, 2021

MAJOR IN HORTICULTURAL SCIENCE AND BIOTECHNOLOGY
DEPARTMENT OF AGRICULTURE, FORESTRY, AND BIORESOURCES
THE GRADUATE SCHOOL OF SEOUL NATIONAL UNIVERSITY

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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

In greenhouses, the higher plant density, the less sunlight inside the canopy due to mutual shadings by adjacent plants. As a countermeasure, inter-lighting has been introduced to compensate for the lack of light in the middle and bottom parts of the canopy. However, most research have focused on growth and yield, not light use efficiency (LUE) and water use efficiency (WUE). The objective of this study was to evaluate the LUE and WUE of sweet peppers subjected to inter-lighting in greenhouses. Two lighting treatments, natural light (control) and supplemental inter-lighting of red and blue LEDs, were applied. The inter-lighting started at 34 days after transplanting (DAT). The ratio of red and blue light in photosynthetic photon flux density (PPFD) was 8:2, and the total PPFD was adjusted to 71 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 20 cm distance. To quantify the transpiration from the plants, the amount of daily transpiration was measured by subtracting the drainage from the supplied nutrient solution, and hydroponic system weight change. The photosynthetic rate was obtained by measuring light response curves at light intensities of 0, 50, 100, 200, 400, 600, 900, 1200, 1500, and 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in PPFD. The LUEs were calculated based on the light interception obtained by 3D-scanned plant models and ray-tracing simulation. The WUEs were calculated using dry weight per accumulated water consumption. The calculated results showed the increase in LUE at the canopy level, which is likely due to the improvement of canopy light distribution by inter-lighting. The WUE for biomass and fruit yield were higher in inter-lighting than those in the control. These results were due to the increases in plant dry weight and fruit yield, which is greater than the increase in water consumption by inter-lighting. In this study, the improvement of LUE and WUE by inter-lighting could be quantified by optical simulation and the water consumption during the whole growth period.

keywords: Intra-canopy lighting, Light use efficiency, Paprika, Photosynthesis, Three-dimensional plant model, Water use efficiency

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INTRODUCTION

Horticultural crop production in greenhouses is an intensive cultivation system with environmental control and systemic planting to increase the crop yield (Qiu et al. 2013). In greenhouses, high planting density could maximize crop yields but intensifies light attenuation as the canopy deepens (Trouwborst et al. 2010). Light provides energy for photosynthesis, and the photosynthetic rate increases as the light intensity increase up to the light saturation point (Linderson et al., 2012).

Light induces stomatal opening to allow a gas exchange for photosynthesis, and wider stomatal pore allows faster diffusion of water vapor from the leaf (i.e., transpiration increases). In cases of low light conditions, however, photosynthesis and transpiration are strongly limited. As the light intensity decreases below light saturation point, the photosynthetic rate drops sharply, whereas the transpiration rate slowly decreases by keeping the stomatal pores open for the respiration of guard cells (Ye et al., 2020).

Inter-lighting (Davis et al., 2016) varies light use efficiency (LUE) and water use efficiency (WUE) due to the change of light distribution of inner canopy, which mediates spatial heterogeneity of photosynthesis and transpiration rate within leaf layers. Since LUE and WUE are important indicators to inter-lighting efficiency, levels of inter-lighting and irrigation for plant production are needed to be optimized by scaling light capture and water consumption. In general, the light distribution in plant canopy under natural light follows the Beer–lambert law (Gholz et al., 1991; James et al., 1995). Thus, photosynthesis and transpiration could be estimated with mathematical models (Cheng et al., 2015; Lee et al., 2018). Canopy light distribution was improved by additional light into middle and lower canopies, but the light distribution under inter-lighting condition is hard to be estimated by interferences between plants, artificial light, and natural irradiance (Paponov et al., 2020; Verheul et al., 2020).

Meanwhile, ray-tracing simulation combined with a three-dimensional (3D) plant model has been used to estimate the light distribution of the plant canopy (Buck-Sorlin et al., 2011; de Visser et al., 2014; Kim et al., 2016). This method could evaluate the amount of light interception by arranging light sources and crop models in a 3D space and calculating the light interception of the canopy for each leaf position (Marrou et al., 2013; Shin et al., 2020). The objective of this study was to quantitatively evaluate the LUE and WUE of sweet peppers under inter-lighting LEDs at different growth stages.

LITERATURE REVIEW

Inter lighting for horticultural crops

Supplemental lighting has been applied in agriculture to compensate for the lack of light (Hao et al., 2012). High-pressure sodium lamps (HPS) are used to increase photosynthetically active radiation in greenhouse crop production. The HPS can only be used as top lighting placed above the crop canopy (Hernández et al., 2015). However, LEDs have a low surface temperature, high energy efficiency, and narrow wavelengths, and thus can be used as inter-lighting within the canopy (Olle et al., 2013; Kumar et al., 2016). Compared to overhead supplemental lighting, inter-lighting constantly provides light to the middle and lower canopy, resulting in more homogeneous light distribution than overhead lighting (Kim et al., 2020). More uniform light distribution increased the LUE in the middle and lower canopy by increasing canopy photosynthesis (Li et al., 2016).

Evaluation of water use efficiency (WUE)

WUE can be calculated by using photosynthesis and transpiration. In general, leaf scale WUE was measured as photosynthetic rate per transpiration rate (Hipólito et al., 2015). Under inter-lighting conditions, the increasing rate in photosynthesis is drastically higher than that in transpiration, resulting in higher WUE (Lanoue et al., 2017). LUE and WUE were estimated from top to bottom canopy in natural light and overhead supplemental lighting environments using mathematical models (Cheng et al., 2015; Lee et al., 2018). However, it is difficult to evaluate LUE and WUE under inter-lighting conditions which provide discontinuous light and complex light distribution, because light sources are installed at the middle canopy for inter-lighting (Paponov et al., 2020; Verheul et al., 2020).

3D analysis of light environments

To examine spatial light distribution within the canopy, ray-tracing simulation with nested radiosity method (Chelle and Andrieu, 1998), Monte Carlo method (Veach, 1997; Cieslack et al., 2008), and reverse ray-tracing method (Bailey, 2018) have been applied. To accurately conduct the ray-tracing simulation, a high-resolution 3D plant model is required. However, most of 3D plant modes had simple structures due to the use of low-resolution of 3D scanners (Buck-Sorlin et al., 2011; de Visser et al., 2014; Kim et al., 2016). With the development of optical technology, high-resolution 3D scanners have been developed, and 3D-scanned models could be implemented to simulate similar to real plants by reconstruction (Paulus et al., 2014; Zhang et al., 2016).

MATERIALS AND METHODS

Plant materials and growth conditions

Experiments were carried out in a Venlo-type greenhouse located at the Seoul National University experimental farm, Suwon (37.3° N, 127.0° E), Korea. The air temperature was maintained at 25–35°C (daytime) and 17–22°C (nighttime) with the roof and sidewall vents. Sweet pepper (*Capsicum annuum* L.) plants were transplanted to rockwool slabs (Grotop, Grodan, Roermond, Netherlands) on March 8, 2021. The cultivation periods ended on July 5, 2021. The plants were grown at a planting density of three plants per m^2 and pruned to maintain two main stems trellised vertically. Until 5–6 nodes appeared after 2 weeks, the open-loop irrigation system with PBG nutrient solution was applied. The EC and pH of the nutrient solution were maintained at 2.6–3.0 dS m^{-1} and 5.5–6.5, respectively. The irrigation system was controlled by the cumulative solar radiation according to Shin et al. (2014). When the cumulative solar radiation reached 50 J cm^{-2}, 133 mL of nutrient solution per dripper was irrigated.

Inter-lighting treatment

Light treatments were divided into natural light without inter-lighting (control) and supplemental lighting of red and blue LEDs (IL). Inter-lighting LEDs were installed at a height of 80 and 100 cm above the slab, after 37 DAT. The ratio of red and blue light in photosynthetic photon flux density (PPFD) was 8:2, and the total PPFD of inter-lighting was adjusted to 71 μmol m^{-2} s^{-1} at a 20 cm distance (Fig. 1A). Forty sweet peppers were grown in each treatment.

Measurement of daily light integral and irrigation amount

Daily light integral was measured at two positions on greenhouse ceilings with a quantum sensor (SQ-110, Apogee Instruments Inc., Logan, Utah, USA) connected to a data logger (Cr-1000, Li-Cor Inc., Lincoln, NE, USA). The automated irrigation control based on the integrated solar irradiance was set to a rate of 116 mL per plant for every 50 MJ m^{-2}. Hydroponic system weight was measured with a single point load cell and drainage scale. The daily water consumption from the plants was determined as irrigation minus drainage using changes in the hydroponic system weight. The weight was logged on server using Raspberry Pi 3 single-board computer Raspberry Pi Foundation, Cambridge, UK) with 1.2 GHz 64-bit quad-core ARMv8 CPU, 802.11n Wireless LAN, Bluetooth 4.1, 4 USB ports, 40 GPIO pins, Ethernet port and Display Interface.

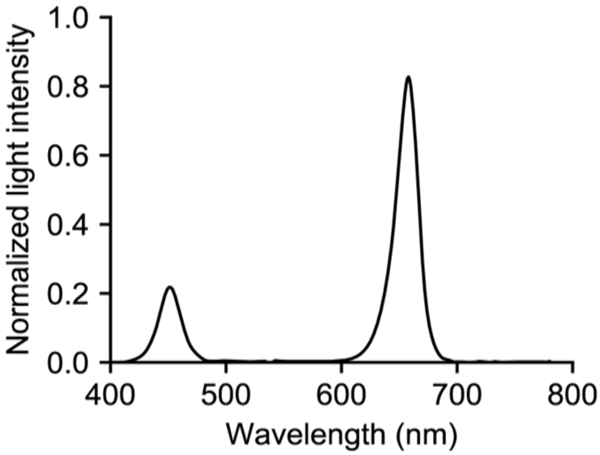

Fig. 1. Spectral distribution of the light source with red (peak at 660nm) and blue (peak at 440nm) light for inter-lighting.

Measurement of leaf photosynthetic rate

Leaf photosynthetic rates were measured using a portable gas exchange system (LI-6400XT; LI-COR Biosciences, Lincoln, NE) equipped with a leaf LED chamber (6400-02B, Li-Cor). The measurements were performed on the top, middle, and lower canopy at 40, 60, 80, 100 and 120 DAT. Before measurement, the leaves were light-adapted at a PPFD of 1,000 μmol m^{-2} s^{-1} for 15 min using a LED light source. The temperature, relative humidity, and CO_2 concentration in the leaf chamber were set at 25°C, 60%, and 400 μmol mol^{-1}, respectively. Photosynthetic light response was measured with a descending gradient of irradiance levels, as follows: 2,000, 1,500, 1,200, 900, 600, 400, 200, 100, 50, and 0 μmol m^{-2} s^{-1}.

Calculation of water use efficiency (WUE) and light use efficiency (LUE)

The WUEs for biomass and fruit yield were determined as the dry weight per cumulative water consumption ($WUE_{biomass}$) (Kadam et al., 2015) and as total fruit yield per cumulative water consumption (WUE_{yield}), respectively:

$WUE_{biomass}$ (g kg^{-1}) = Total dry weight (g $plant^{-1}$) / Cumulative water consumption (kg $plant^{-1}$) -- (1)

WUE_{yield} (g kg^{-1}) = Total fruit yield (g $plant^{-1}$) / Cumulative water consumption (kg $plant^{-1}$) -- (2)

The LUE was calculated as plant photosynthetic rate per quantity of light intercepted by the plant, which was obtained by ray-tracing simulation using 3D plant models described below.

Measurement of growth and morphological characteristics

Average plant height and fresh weight of organ (stem, leaf, and petiole) were measured with randomly extracted five plants on 40, 60, 80, 100 and 120 DAT. Fruit weights were measured individually throughout the experiment when fully colored yellow. Fruit yield was determined as the cumulative fruit weight per plants (g plant^{-1}). Dry weights of each organ were obtained after drying in an oven at 80°C for 99 h. Leaf area was measured using ImageJ software (US National Institutes of Health, Bethesda, MD, USA).

Ray-tracing simulation with 3D-scanned plant models

3D-scanned models were directly obtained by 3D scanning of plants grown under sunlight (Control) and additional inter-lighting with red and blue LEDs (IL) at 40, 60, 80, 100 and 120 DAT (Fig. 2A) using a high-resolution portable 3D scanner (GO!SCAN50TM, CREAFORM, Lévis, Quebec, Canada) and scan software (VXelement 6.0, CREAFORM). The resolution of the 3D scanner was set to 0.5 mm. Before 3D scanning, the scanner was calibrated to the ambient light environment in the greenhouse with a calibration plate and circular retro-reflective stickers were affixed to the plant to provide the scanner with the object 3D-reference positioning information. After scanning the sweet pepper plants, scanned mesh data were manually segmented into individual leaves, stems, and fruits, while imperfections such as holes and floating fragments were corrected with reverse engineering software (Geomagic Design X, 3D Systems, Rock Hill, SC, USA). After preprocessing of the mesh data, the leaf rea of the scanned mesh was extracted. The scanned mesh was converted to a PM to perform optical simulations with the same software (Fig. 2B). Constructed 3D plant models were transferred to a 3D CAD software (SOLIDWORKS, Dassault Systemes, Vélizy-Villacoublay, France).

From simulated results, light interception was defined as absorbed photosynthetically active photon per unit area per unit time on plant surface. All simulations were performed hourly from 6:00 to 18:00. The plants were arranged in 3 × 3 isotropic form, and the row distance of individual plants was set to 40 cm. Leaf area was measured by ImageJ software (US National Institutes of Health, Bethesda, Maryland, USA) to compare the actual leaf area with the leaf area derived from the scanned mesh.

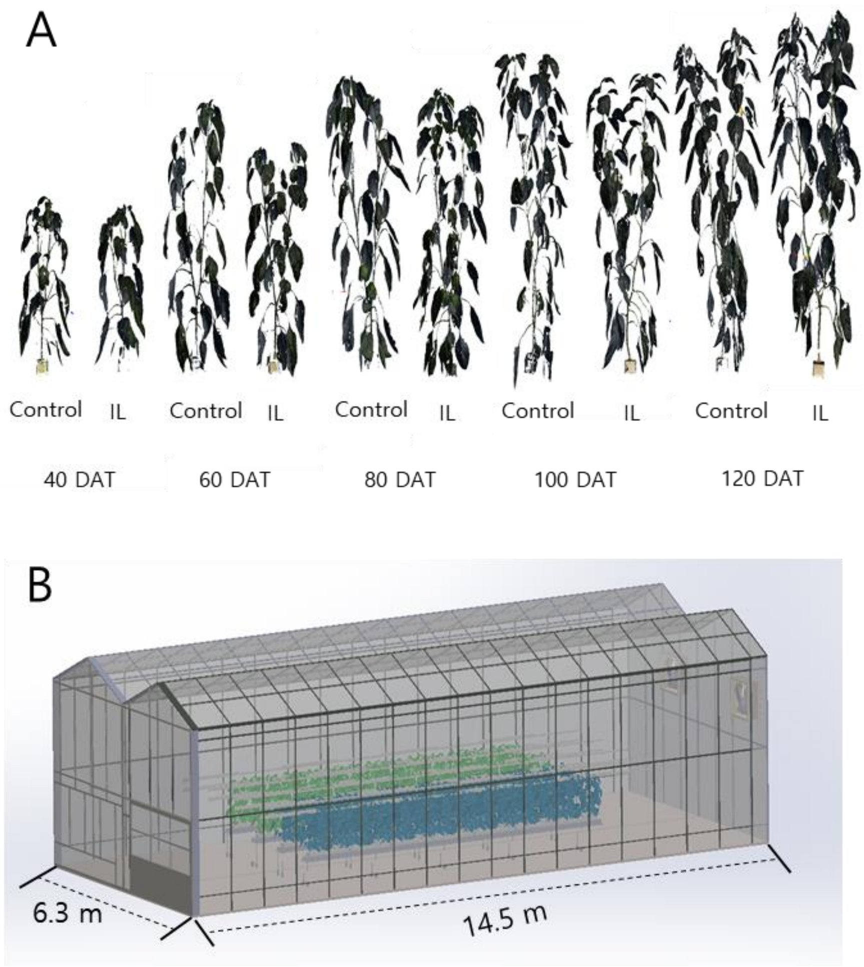

Fig 2. 3D-scanned models of sweet peppers at 40, 60, 80, 100 and 120 days after transplanting (DAT) grown under sunlight (Control) and additional inter-lighting with red and blue LEDs (IL) (A), and a Venlo-type greenhouse with the 3D plant models constructed for ray-tracing simulation (B).

Calculation of photosynthetic rate using simulated light distribution

Photosynthetic rate of the plants was calculated by non-rectangular hyperbolic model (Prioul and Chartier, 1977, Retkute et al, 2015).

$$P(L, P_{max}) = \phi L + (1 + \alpha)P_{max} - \alpha P_{max}$$

where, L is the PPFD incident on a leaf (μmol m^{-2} s^{-1}), ϕ is the maximum quantum yield, α corresponds to the fraction of the maximum photosynthetic capacity used for dark respiration, and the parameter θ determines the curvature of the light-response curve (Table 1).

Statistical analysis

Multiple mean comparisons among the different treatments were performed student's t-test using SPSS statistics, version 25.0 (IBM Corp., Armonk, NY, USA). The statistical level of significance was chosen at $P < 0.05$ for all statistical analyses.

Table 1. Estimated parameters of the rectangular hyperbolic photosynthetic model from light-response curve measurements at 40, 60, 80, 100 and 120 days after transplanting (DAT) in the control and the inter-lighting with red and blue LEDs (IL).

Treatment	Location	DAT	Parameter			
			P_{max}	ϕ	α	Θ
Control	Top	40	-	-	-	-
		60	20.96	0.042	0.017	0.934
		80	22.65	0.037	0.016	0.953
		100	15.38	0.974	0.013	0.0.974
		120	18.08	0.033	0.020	0.966
	Middle	40	15.00	0.047	0.029	0.931
		60	13.08	0.056	0.041	0.911
		80	18.98	0.040	0.015	0.951
		100	9.13	0.976	0.073	0.971
		120	7.67	0.012	-0.06	0.951
	Lower	40	12.16	0.053	0.044	0.917
		60	9.09	0.071	0.024	0.833
		80	9.3	0.062	0.049	0.906
		100	4.76	0.967	0.050	0.967
		120	3.97	0.009	0.051	0.954
IL	Top	40	-	-	-	-
		60	20.75	0.046	0.009	0.914
		80	23.01	0.038	0.034	0.951
		100	17.51	0.956	0.053	0.956
		120	18.77	0.033	0.024	0.968
	Middle	40	19.69	0.043	0.024	0.920

	60	14.89	0.045	0.015	0.955
	80	19.73	0.052	0.008	0.912
	100	10.98	0.971	0.009	0.968
	120	11.68	0.019	-0.042	0.958
Lower	40	15.00	0.047	0.029	0.956
	60	11.39	0.052	0.025	0.929
	80	11.85	0.067	0.066	0.927
	100	6.32	0.951	0.025	0.951
	120	5.69	0.015	-0.023	0.945

RESULTS

Simulated light interception

Under the natural light, no significant difference in light interception was observed among 40, 60, and 80 DAT (Table 2). However, under the NL with AL condition, the light interception increased by 29%, 25%, 41%, 41% and 39% at 40, 60, 80 100 and 120 DAT in IL, respectively. The photosynthetic rate significantly increased by 21%, 22%, 31%, 39% and 54% at 40, 60, 80, 100 and 120 DAT in IL, respectively. The LUE was significantly higher in the control at 40, 60, 80 and 100 DAT under the natural light condition. Under the NL+AL conditions, additional light absorption from the AL condition increased the LUE, which was significantly higher than the control by 15%, 24%, 37%, 62% and 74% at 40, 60, 80, 100 and 120 DAT, respectively.

Table 2. Simulated light interception, photosynthetic rate, and light use efficiency (LUE) obtained by using 3D-scanned plant models and ray-tracing simulation at 40, 60, 80, 100 and 120 days after transplanting (DAT) in the control and inter-lighting with red and blue LEDs (IL).

Treatment	DAT	Light interception (μmol plant^{-1} s^{-1})		Photosynthetic rate (μmol CO_2 s^{-1} plant^{-1})	LUE (g DM mol^{-1} s^{-1} absorbed PAR from NL)	LUE (g DM mol^{-1} s^{-1} absorbed PAR from AL)
		NL	AL			
Control	40	47.73±4.19	-	3.56±0.11	3.30±0.20	-
	60	73.17±13	-	4.17±0.56	2.53±0.14	-
	80	113.39±25.56	-	4.2±0.41	1.38±0.05	-
	100	116.83±8.51	-	2.77±0.23	1.05±0.09	-
	120	98.86±11.71	-	1.36±0.21	0.61±0.08	-
IL	40	52.91±5.97	13.85±2.78**	4.53±0.29**	2.80±0.18	1.09±0.24*
	60	73.88±8.47	23.48±3.66**	5.36±0.0.37**	2.16±0.06	1.15±0.2**
	80	117.27±11.6	75±8.01**	6.09±0.34**	0.87±0.04	1.33±0.09**
	100	122.52±30.54	76.86±11.19**	4.57±0.64**	0.95±0.28	1.85±0.94**
	120	115.97±19.92	48.00±31.55**	2.96±0.39**	0.71±0.08	1.63±1.07**

*Statistical analysis was performed using Student's t-test (n=5). *indicates $P < 0.05$, **indicates $P < 0.01$.

*NL: Natural light, *AL: Artificial light, *IL: Inter-lighting

Photosynthetic capacity with inter-lighting

Up to 40 DAT, the plants did not reach the height of the IL, and thus the light curves were measured for only two parts of the top and lower canopy (Fig. 3A, 3B). Overall, there was no significant difference in photosynthetic capacity between the control and IL at 40, 60 and 120 DAT (Fig. 3A-3E). However, as the growth progressed, the difference in photosynthesis capacity of the middle and lower canopy increased until 80 DAT. The middle canopy was significantly higher at a light intensity over 400 μmol m^{-2} s^{-1}, and the lower canopy showed a significant difference at a low light intensity between 100 and 400 μmol m^{-2} s^{-1} in IL (Fig. 3G, 3H). At 100 DAT, the middle canopy was significantly higher at 600, 1200, 1500, and 2000 μmol m^{-2} s^{-1} in IL, while the lower canopy was significantly higher at 1500 μmol m^{-2} s^{-1} in IL.

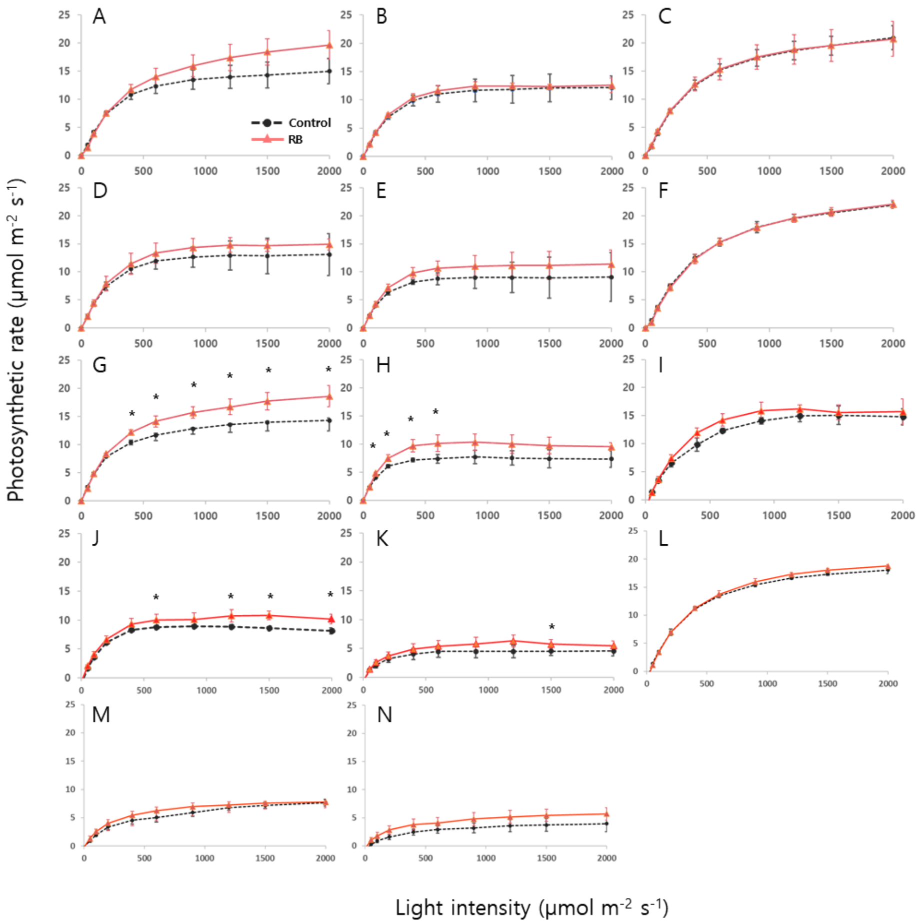

Fig 3. Photosynthetic rate of sweet pepper leaves to light intensities in the control (Control) and inter-lighting with red and blue LEDs (IL). A and B are the measured results at the top and lower canopies at 40 days after transplanting (DAT); C, D, and E are the results at the top, middle, and lower canopies at 60 DAT; and F, G, and H are the results at the top, middle, and lower canopies at 80 DAT; and I, J and K are the results at the top, middle, and lower canopies at 100 DAT; and L, M, N are the results at the top, middle, and lower canopies at 120 DAT respectively. Vertical bars indicate the mean ± SD (n=3).

Growth and morphological characteristics with growth stage

The plant height was not significantly different between the treatments at 40 and 120 DAT, however those in the control was significantly higher than in IL at 60, 80 and 100 DAT (Table 3). The leaf area in the control was significantly higher than that in IL at 60 DAT. The leaf dry weight increased by 11%, 4%, 16%, and 2% at 40, 60, 80 and 120 DAT, respectively, and significantly increased by 17% at 100 DAT in IL. The stem dry weight increased by 5% and 4% at 40 and 100 DAT in IL, increased by 3%, 4% and 1% at 60, 80 and 120 DAT, respectively in the control but there was no significant differences. The petiole dry weight increased by 13% and 4% at 40 and 80 DAT, increased by 4%, 13% and 4% at 60, 100 and 120 DAT, respectively, in IL. The total dry weight increased by 5.3%, 3.3%, 1%, 11% and 2% at 40, 60, 80, 100 and 120 DAT in IL, respectively, but there was no significant difference. The leaf mass per area (LMA) showed no significant difference at 40 and 120 DAT, however significantly increased by 13%, 15% and 15% at 60, 80 and 100 DAT, respectively, in IL than in the control.

Table 3. Comparison of plant height, leaf area, leaf mass per area (LMA), and organ dry weight between the control and inter-lighting with red and blue LEDs (IL) at 40, 60, 80, 100 and 120 days after transplanting (DAT).

Treatment	DAT	Plant height (cm)	Leaf area (m^2 $plant^{-1}$)	Dry weight (g $plant^{-1}$)			Total dry weight (g $plant^{-1}$)	LMA (g m^{-2} $plant^{-1}$)
				Leaf	Stem	Petiole		
Control	40	80.96±4.09	0.41±0.01	11.98±0.71	11.13±0.58	2.11±0.25	25.17±1.62	29.37±0.88
	60	124.4±5.77*	0.62±0.02*	24.55±1.12	24.55±1.2	5.74±0.28	53.74±2.65	39.64±0.45
	80	133.7±3.64*	0.86±0.06	31.04±3.49	35.12±3.94	7.22±0.88	75.77±8.43	35.96±1.45
	100	168.8±6.58*	1.02±0.09	38.96±5.28	45.32±8.08	9.02±0.92	93.3±13.52	37.93±1.84
	120	170.6±10.43	0.94±0.07	50.45±4.90	64.10±8.55	11.37±1.20	125.91±13.56	53.56±3.13
IL	40	74.68±5.02	0.44±0.028	13.45±0.43	11.68±0.83	1.83±0.22	26.59±1.21	30.65±1.42
	60	116.8±2.492	0.56±0.01	25.53±1.18	23.93±3.60	5.95±6.49	55.53±4.19	45.37±2.48*
	80	123±6.31	0.88±0.07	37.01±3.19	33.73±2.16	6.91±0.63	76.42±4.81	42.09±1.16**
	100	153.4±10.97	1.05±0.05	47.07±3.22*	47.31±6.48	10.32±0.54*	104.7±10.65	44.61±1.95**
	120	168.1±12.38	0.93±0.10	52.50±6.73	63.61±10.23	11.83±2.32	127.94±18.60	53.44±6.62

*Statistical analysis was performed using Student's t-test (n=5). *indicates $P < 0.05$, **indicates P<0.01

Water use efficiency with inter-lighting with growth stage

As the plant growth progressed, the daily water consumption increased in both treatments (Fig. 4A). The accumulated water consumption in IL was higher by 1%, 4%, 5%, 3%, and 3% at 40, 60, 80, 100 and 120 DAT, respectively, than in the control, but not significant (Fig. 4B). The $WUE_{biomass}$ in IL increased by 6%, 1%, and 7% at 40, 60, and 100 DAT, respectively, than in the control, while the $WUE_{biomass}$ in the control increased by 5% and 1% at 80 and 120 DAT, respectively, but not significant (Fig. 5). The $WUE_{biomass}$ tend to decrease both in the control and IL as the crop period progressed, but not significant. The WUE_{yield} significantly increased by 23% in IL than in the control (Fig. 6).

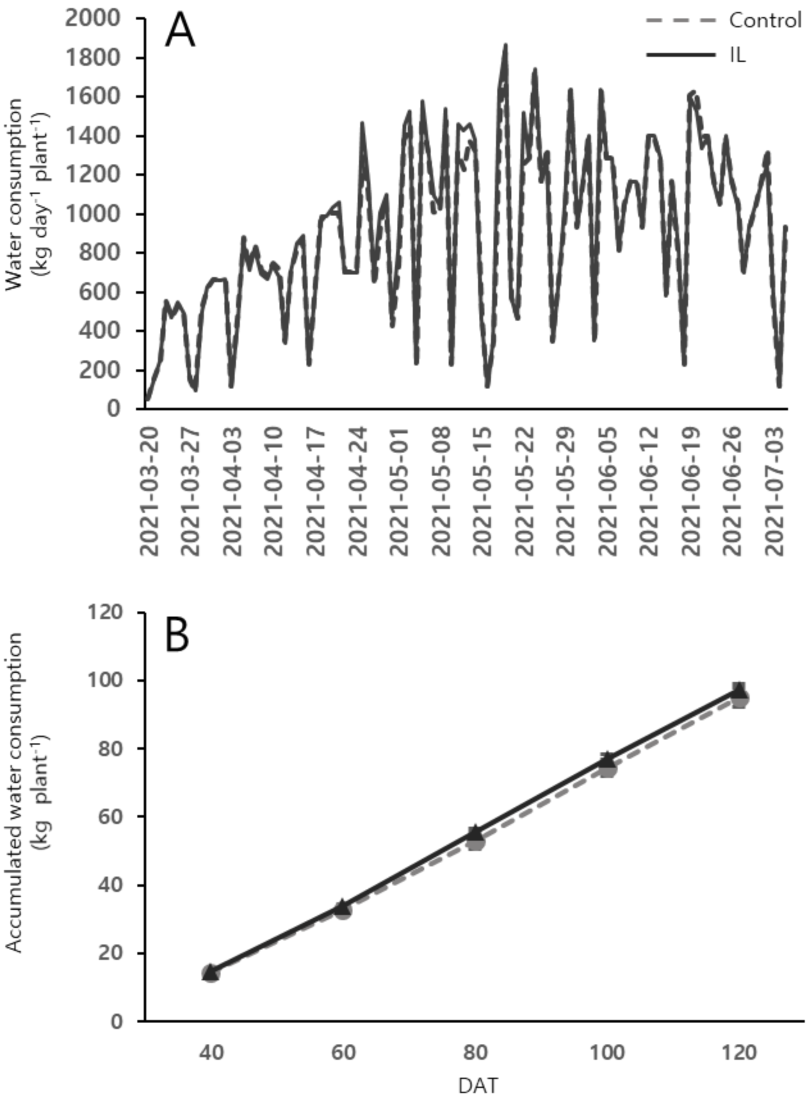

Fig 4. Daily measured water consumption (A) and accumulated water consumption at 40, 60, 80, 100 and 120 days after transplanting (DAT) (B) in the control and inter-lighting with red and blue LEDs (IL) during the cultivation period.

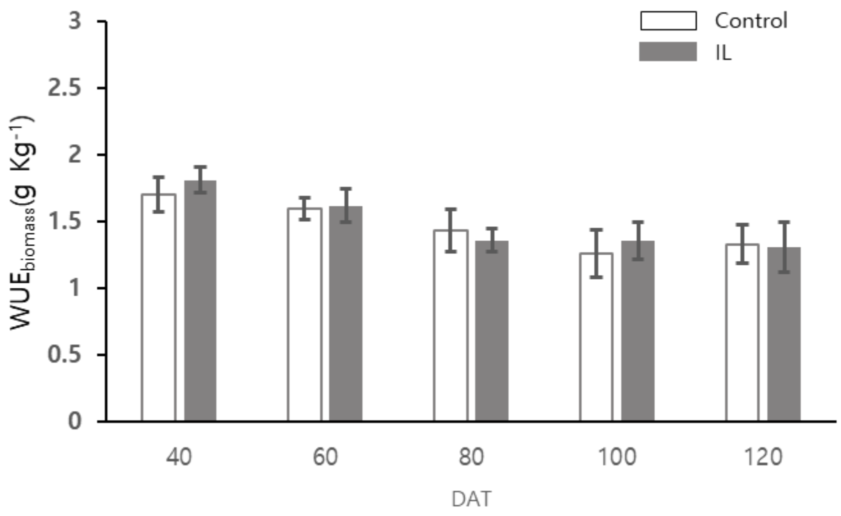

Fig 5. Water use efficiency for biomass (WUE$_{biomass}$) at 40, 60, 80, 100, and 120 days after transplanting (DAT) in the control and inter-lighting with red and blue LEDs (IL). Vertical bars indicate the mean ± SD (n=5).

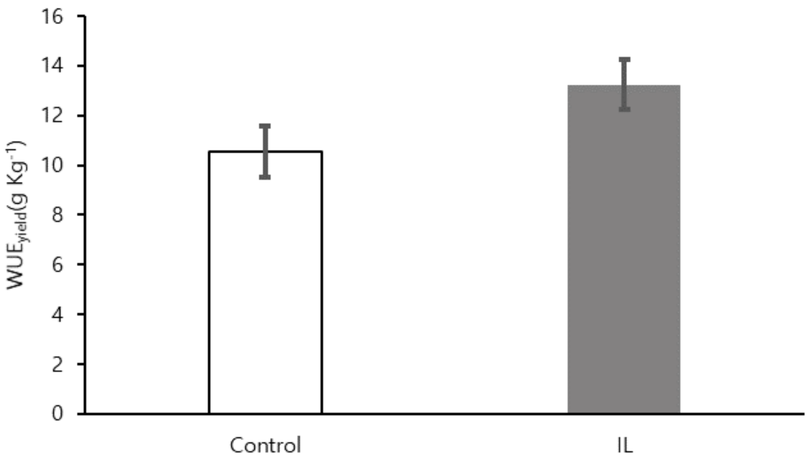

Fig 6. Water use efficiency for yield (WUE_{yield}) in the control and inter-lighting with red and blue LEDs (IL). Vertical bars indicate the mean ± SD (n=5).

DISCUSSION

Inter-lighting increased light use efficiency

In this study, the light use efficiency, which can be defined as the ratio of biomass production per unit light interception (Yusuke et al., 2014), decreased in both the control and IL. As a reason of decreased LUE, the simulation results indicate that light interception increase and photosynthetic rate decrease due to the increase in plant height with growth stage, as reported by Mao et al. (2014). However, the LUE of the middle and lower canopies was relatively higher in IL than in the control as the growth progressed (Table 2). It seems that the contribution of IL was greater due to the lack of light in the middle and lower canopy according to the growth stage. In greenhouses, most of the sunlight is absorbed by leaves at the top canopy due to high planting density. However, the upper leaves cannot efficiently utilize strong light for photosynthesis because leaf photosynthetic rates are saturated at a high PPFD (Gu et al., 2003). Photosynthesis above the light saturation point decrease LUE (Koyama et al., 2010). However, inter-lighting generally provides PPFD below the saturation point, so leaf-level LUE for photosynthesis can be higher (Pearcy et al., 1990). Therefore, these results could support that inter-lighting increases the LUE by improving the photosynthetic rate at the middle and lower canopy.

Inter-lighting improved photosynthetic rate

Leaf photosynthetic capacity is closely related with its spatial position (Kim et al., 2016）. Inter-lighting did not affect the photosynthetic capacity of the top canopy. However, in the middle and lower canopy, there were significant differences between the control and IL at 80 and 100 DAT, and no difference at 120 DAT due to leaf senescence. Lim and Park (2018) reported that in the natural light, higher leaf spectral transmittance of far-red light increases the far-red to red ratio (FR: R) from top to bottom canopy. Higher FR: R ratio caused premature senescence of the leaves (Paponov et al. 2019). Our results indicates that IL reduces the FR: R ratio and increased the light amounts of the middle or lower canopy to prevent the leaf senescence and improve the photosynthesis rate at 80 and 100 DAT, but showed no effect after 120 DAT.

Inter-lighting affected plant biomass and morphology

The leaf area was not influenced by IL (Table 3) but higher partitioning of assimilates toward leaves was clearly visible in the LMA, which was significantly higher at 60, 80, and 100 DAT in IL. Kim (2019) reported that the LMA, acclimation response of leaves, is affected by light intensity and light quality. Evans and porter (2001) reported that the LMA was higher in a higher light intensity during leaf development Hogewoning and Trouwborst (2010) reported that a greater fraction or absolute amount of blue light is generally associated with the development of 'sun-type' leaves, which are characterized by leaves with a high LMA (Buschmann et al., 1978; Lichtenthaler et al., 1980; Matsuda et al., 2008). Claypool and Scientia (2020) reported the reduction in plant height by blue light. From the previous results as above, shorter plant height and greater LMA in IL at 60, 80, and 100 DAT seems to be due to the blue light in this study. However, after 120 DAT, leaf senescence caused the decrease in leaf area in both the control and IL due to deciduous phenomenon in the middle and lower canopy, and there was no significant difference in leaf dry weight and LMA in the control and IL.

Inter-lighting increased water use efficiency

In this study, inter-lighting increased the WUE_{yield} with fruit yields higher than cumulative water consumption. Novriyanti and Watanave (2012) reported that there was a positive correlation between WUE and LMA. A higher LMA with thicker and more compact tissue could enhance water diffusion resistance (Givnish 1998). Li and Liu (2019) reported supplemental lighting improved WUE via regulating the trade-off between photosynthetic carbon gain and transpired water. Li et al. (2008) reported the increase in LUE has a positive effect on an increase in WUE. Therefore, the inter-lighting increased the WUE without an additional amount of water consumption by improving the plant photosynthetic capacity, LUE, and LMA in the middle and lower canopy in this study.

CONCLUSION

In this study, the effect of inter-lighting on water use efficiency (WUE) and light use efficiency (LUE) was analyzed with growth stage. In general, light interception tended to decrease as growth progressed. The inter-lighting increased the photosynthetic rates of the middle and lower canopies than the control, resulting in the increases in LUE and leaf mass per area (LMA), which improved the WUE_{yield} with higher yield than water consumption. This result can be used to determine the effects of inter-lighting on plant growth and transpiration in terms of LUE and WUE, respectively, in greenhouses.

LITERATURE CITED

Bailey BN (2018) A reverse ray-tracing method for modelling the net radiative flux in leaf-resolving plant canopy simulations. Ecological Modelling 368: 233-245.

Buschmann C, Meier D, Kleudgen HK, Lichtenthaler HK (1978) Regulation of chloroplast development by red and blue light. Annual European Symposium on Photomorphogenesis 195-198.

Buck-Sorlin G, de Visser PHB, Henke M., Sarlikioti V, van der Heijden GW, Marcelis LFM, Vos J (2011) Towards a functional–structural plant model of cutrose: simulation of light environment, light absorption, photosynthesis and interference with the plant structure. Annals of Botany 108:1121–1134.

Chelle M, Andrieu B (1998) The nested radiosity model for the distribution of light within plant canopies. Ecological Modelling 111:75-91.

Cheng SJ, Bohrer G, Steiner AL, Hollinger DY, Suyker A, Phillips RP, Nadelhoffer KJ (2015) Variations in the influence of diffuse light on gross primary productivity in temperate ecosystems. Agricultural and Forest Meteorology 201:98-110.

Cieslak M, Lemieux C, Hanan J, Prusinkiewicz P (2008) Quasi-Monte Carlo simulation of the light environment of plants. Functional Plant Biology 35: 837-849.

Claypool NB, Lieth JH (2020) Physiological responses of pepper seedlings to various ratios of blue, green, and red light using LED lamps. Scientia Horticulturae 268:109371.

Davis PA, Burns C (2016) Photobiology in protected horticulture. Food Energy Security 5:223–238.

De Visser PH, Buck-Sorlin GH, van der Heijden GW (2014). Optimizing illumination in the greenhouse using a 3D model of tomato and a ray tracer. Frontiers in Plant Science 5:48.

Díaz-Pérez JC, Hook JE (2017) Plastic-mulched bell pepper (*Capsicum annuum* L.) plant growth and fruit yield and quality as influenced by irrigation rate and calcium fertilization. Horticultural Science 52:774-781.

Evans JR, Poorter H (2001) Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant, Cell & Environment 24:755-767.

Gholz HL, Vogel SA, Cropper WP, McKelvey KC, Ewel RO, Teskey PJ (1991) Dynamics of canopy structure and light interception in *Pinus Elliottii* Stands, North Florida. Curran Ecological Monographs 61:33-51.

Givnish T (1988) Adaptation to sun and shade: A whole-plant perspective. Functional Plant Biology 15:63-92.

Gu L, Baldocchi DD, Wofsy SC, Munger JW, Michalsky JJ, Urbanski SP, Boden TA (2003) Response of a deciduous forest to the Mount Pinatubo eruption: enhanced photosynthesis. Science 299:2035–2038.

Hao X, Zheng JM, Little C, Khosla S (2012) LED inter-lighting in year-round greenhouse mini-cucumber production. Acta Horticulturae 956:335-340.

Hernández R, Kubota C (2015). Physiological, morphological, and energy-use efficiency comparisons of LED and HPS supplemental lighting for cucumber transplant production. Horticultural Science 50:351-357.

Hipólito M, Magdalena T, Sebastià M, Jaume F, Esther H, Joan R, Alicia P, José-Mariano E, Josefina B (2015) From leaf to whole-plant water use efficiency (WUE) in complex canopies: Limitations of leaf WUE as a selection target. The Crop Journal 3:220-228.

Hogewoning SW, Trouwborst G, Maljaars H, Poorter H, Ieperen WV, Harbinson J (2010) Blue light dose–responses of leaf photosynthesis, morphology, and chemical composition of *Cucumis sativus* grown under different combinations of red and blue light. Journal of Experimental Botany 61:3107–3117.

James MV, Barton DC, Sullivan NH, Paul VB (1995) Vertical leaf area distribution, light transmittance, and application of the Beer–Lambert Law in four mature hardwood stands in the southern Appalachians. Canadian Journal of Forest Research 25:1036-1043.

Kadam N, Yin X, Bindraban P, Struik P, Jagadish K (2015) Does morphological and anatomical plasticity during the vegetative stage make wheat more tolerant of water-deficit stress than rice?. Plant Physiology 167:1389-1401.

Kim DP, Kang WH, Hwang IH, Kim JW, Kim JH, Park KS, Son JE (2020) Use of structurally-accurate 3D plant models for estimating light interception and photosynthesis of sweet pepper (*Capsicum annuum*) plants. Computers and Electronics in Agriculture 177:105689.

Kim HJ, Lin MY, Mitchell CA (2019) Light spectral and thermal properties govern biomass allocation in tomato through morphological and physiological changes. Environmental and Experimental Botany 157:228-240

Kim JH, Lee JW, Ahn TI, Shin JH, Park KS Son JE (2016) Sweet pepper (*Capsicum annuum* L.) canopy photosynthesis modeling using 3D plant architecture and light ray-tracing. Frontiers in Plant Science 7:1321.

Koyama K, Kikuzawa K. Geometrical similarity analysis of photosynthetic light response curves, light saturation and light use efficiency. Oecologia 164:53–63

Kumar KGS, Hao X, Khosla S, Guo X, Bennett N (2016). Comparison of HPS lighting and hybrid lighting with top HPS and intra-canopy LED lighting for high-wire mini-cucumber production. Acta Horticulturae 1134:111-118.

Lanoue J, Evangelos D, Leonardos, Xiao M, Bernard G (2017) The Effect of spectral quality on daily patterns of gas exchange, biomass gain, and water-use-efficiency in tomatoes and *Lisianthus*: An assessment of whole plant measurements. Frontiers in Plant Science 8:1076.

Lee MS, Hollinger DY, Keenan TF, Ouimette AP, Ollinger SV, Richardson AD (2018) Model-based analysis of the impact of diffuse radiation on CO2 exchange in a temperate deciduous forest. Agriculture Forest Meteorology 249: 377–389.

Li K, Li Z and Yang Q (2016) Improving light distribution by zoom lens for electricity savings in a plant factory with light-emitting diodes. Frontiers in Plant Science 7:92.

Li Q, Liu Y, Tian S, Liang Z, Li S Li Y, Wei M, Zhang D (2019) Effect of supplemental lighting on water transport, photosynthetic carbon gain and water use efficiency in greenhouse tomato. Scientia Horticulturae 256:108630.

Li SG, Eugster W, Asanuma J, Kotani A, Davaa G, Oyunbaatar D, Sugita M (2008) Response of gross ecosystem productivity, light use efficiency, and water use efficiency of Mongolian steppe to seasonal variations in soil moisture. Journal of Geophysical Research 113:G1.

Lichtenthaler HK, Buschmann C, Rahmsdorf U (1980) The Importance of blue light for the development of sun-type chloroplasts. The Blue Light Syndrome pp:485-494.

Lim J, Park JH, Jung SJ, Hwang DH, Nam HG, Hong SH (2018) Antagonistic roles of PhyA and PhyB in far-red light-dependent leaf senescence in *Arabidopsis thaliana*. Plant and Cell Physiology 59:1753-1764.

Linderson ML, Mikkelsena TN, Ibroma A, Lindrothb H, Poulsenc RO, Pilegaarda K (2012) Up-scaling of water use efficiency from leaf to canopy as based on leaf gas exchange relationships and the modeled in-canopy light distribution. Agricultural and Forest Meteorology 152:201-211.

Mao L, Zhang L, Zhao X, Liu S, Werf WVD, Zhang S, Spiertz H, Li Z (2014) Crop growth, light utilization and yield of relay intercropped cotton as affected by plant density and a plant growth regulator. Field Crops Research 155:67-76.

Marrou H, Wéry J, Dufour L, Dupraz C (2013) Productivity and radiation use efficiency of lettuces grown in the partial shade of photovoltaic panels. European Journal of Agronomy 44:54-66.

Matsuda R, Ohashi-Kaneko K, Fujiwara K, Kurata K (2008) Effects of blue light deficiency on acclimation of light energy partitioning in PSII and CO2 assimilation capacity to high irradiance in spinach leaves. Plant and Cell Physiology 49:664-670.

Novriyantie, Watanabe M, Makoto K, Takeda T, Hashidoko Y, Koike T (2012) Photosynthetic nitrogen and water use efficiency of acacia and eucalypt seedlings as afforestation species. Photosynthetica 50:273-281.

Olle M and Viršile A (2013). The effects of light-emitting diode lighting on greenhouse plant growth and quality. Agricultural and Food Science 22:223–234.

Paponov M, Kechasov D, Lacek J, Verheul M, Paponov J (2019) Supplemental light-emitting diode Inter-lighting increases tomato fruit growth through enhanced photosynthetic light use efficiency and modulated root activity. Frontiers in Plant Science 10:1656.

Paulus S, Schumann H, Kuhlmann H, Léon J (2014) High-precision laser scanning system for capturing 3D plant architecture and analyzing growth of cereal plants. Biosystems Engineering 121:1-11.

Pearcy RW (1990) Sunflecks and photosynthesis in plant canopies. Annual Review of Plant Biology 41:421–453.

Prioul JL, Chartier P (1977) Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO_2 fixation: A critical analysis of the methods used. Annals of Botany 41:789–800.

Qiu R, Song J, Du T, Kang S, Tong L, Chen R (2013) Response of evapotranspiration and yield to planting density of solar greenhouse grown tomato in northwest China. Agricultural Water Management 130:44-51.

Retkute R, Stephanie ES, Robert WS, Alexandra JB, Oliver EJ, Giles NJ, Simon PP, Erik HM (2015) Exploiting heterogeneous environments: does photosynthetic acclimation optimize carbon gain in fluctuating light?. Journal of Experimental Botany. 66:2437–2447.

Sánchez AR, Aranda RR, Cuartero J (2005) Plant water uptake and water use efficiency of greenhouse tomato cultivars irrigated with saline water. Agricultural Water Management 78:54-6.

Shin JH, Park JS, Son JE (2014) Estimating the actual transpiration rate with compensated levels of accumulated radiation for the efficient irrigation of soilless cultures of paprika plants. Agricultural Water Management 135:9-18.

Shin JY, Hwang IH, Kim DP, Moon TW, Kim JW, 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 ray-tracing simulation. Agricultural and Forest Meteorology 296:108219.

Splinter WE (1974) Modelling of plant growth for yield prediction. Agricultural Meteorology. 14:243-253.

Trouwborst G, Hogewoning S, van Kooten O, Harbinson J, van Ieperen W (2016) Plasticity of photosynthesis after the “red light syndrome” in cucumber. Environmental and Experimental Botany 121:75–82.

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 & Environment. 34:1563-1576.

Veach, E, Guibas LJ (1997) Robust Monte Carlo methods for light transport simulation. Stanford University. Dissertation.

Verheul MJ, Maessen HFR, Panosyan A, Naseer M, Paponov M, Paponov IA (2019) Effects of supplemental lighting and temperature on summer production of tomato in Norway. Acta Horticulturae 1296:707-174.

Ye ZP, Ling Y, Yu Q, Duan H-L, Kang H-J, Huang G-M, Duan S-H, Chen X-M, Liu Y-G and Zhou S-X (2020) Quantifying light response of leaf-scale water-use efficiency and its interrelationships with photosynthesis and stomatal conductance in C3 and C4 species. Frontiers in Plant Science 11:374.

Yusuke O, Jema BS, Kosuke A, Shin-ichiro A, Tetsukazu Y, Niels PRA (2014) Trade-off between light interception efficiency and light use efficiency: implications for species coexistence in one-sided light competition. Journal of Ecology. 102:167-175.

Zhang Y, Teng P, Shimizu Y, Hosoi F, Omasa K (2016) Estimating 3D leaf and stem shape of nursery paprika plants by a novel multi-camera photography system. Sensors 16:874.

ABSTRACT IN KOREAN

온실에서는 재식밀도가 높아질수록 인접한 식물간의 간섭 현상으로 캐노피 내부에 빛이 부족하게 된다. 이에 대한 대책으로 군락 중, 하단부의 빛 부족을 보완하기 위해 군락 내 보광을 도입하고 있다. 현재 대부분의 연구는 광이용 효율(LUE), 물이용 효율(WUE)이 아닌 생장과 수확량에 초점을 맞추어 왔다. 따라서 이 연구의 목적은 온실에서 군락 내 측면 보광(inter−lighting) 하에서 자란 파프리카의 LUE 와 WUE 를 평가하는 것이다. 자연광(대조구)과 자연광에 적색 및 청색 LED 에 의한 보광 처리구가 적용되었다. 보광 처리는 정식 후 34 일 (DAT)에 시작하였고, 적색 및 청색 LED 비율이 8:2 인 광원은 20cm 거리에서 71μmol · m^{-2} · s^{-1}로 설정하였다. 식물의 증산량을 정량화 하기 위해 수경재배 무게측정 시스템으로 급액량에서 배액량을 제하여 하루 증산량을 측정했다. 광합성속도는 0, 50, 100, 200, 400, 600, 900, 1200, 1500, 2000 μmol · m^{-2} · s^{-1}에서 광반응 곡선을 측정하여 얻었다. LUE 는 40, 60, 80, 100 및 120 DAT 에서 3D 식물 모델 및 광학 시뮬레이션으로 측정한 수광 태세를 기반으로 계산하였다. WUE 는 40, 60, 80, 100 및 120 DAT 에서 누적된 물 소비량 대비

건조중으로 계산하였다. 시뮬레이션 결과에서 캐노피 수준의 LUE 가 증가하였는데, 이는 보광 이 캐노피 내부의 수광 개선에 기인한 것으로 보인다. 건물중 및 과일 생산량에 대한 WUE 는 대조군보다 보광 처리구에서 더 높았다. 이러한 결과는 보광에 의한 물 소비보다 식물의 건조 중량과 과일 수확량의 증가폭이 더 높았기 때문이다. 본 연구에서는 광학 시뮬레이션과 전체 생장 기간 동안의 물 이용량을 분석하여 군락 내 측면 보광으로 인한 LUE 및 WUE 증가를 정량화 할 수 있게 되었다.

주요어: 광합성, 빛 이용 효율, 수관 내부 보광, 파프리카, 3 차원 식물 모델

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