Enhancing Radiation-Use Efficacy of Dwarf Tomato Cultivation in a Plant Factory with Artificial Light

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（千葉大学審査学位論文）

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CHAPTER 1.

Introduction

1.1. Advantages of dwarf tomatoes in a plant factory with artificial light

Tomatoes are one of the world's major fresh and processed fruits and are the second most important vegetable crop worldwide (Costa and Heuvelink, 2018).

Recently, there have been several new demands for tomato production (Costa and Heuvelink, 2018). Firstly, the tomato processing market is being driven by the increasing consumption of processed tomatoes globally. Secondly, to reduce loss generated by long-distance transport, tomato production should be conducted in the vicinity of urban areas and the market. Thirdly, environmentally friendly production of tomatoes should be more efficient in use of water, nutrients, and energy. In order to meet such demands, the production system should be improved.

The plant factory with artificial light (PFAL) is used in many countries for commercial production of leaf vegetables, herbs, and transplants. Compared with open fields or greenhouses, PFALs have many potential advantages (Kozai and Niu, 2019). Commercial PFALs should maintain high space utilization efficiency in a cultivation room to reduce production costs. Because the distance between vertical tiers is typically around 40 cm, plants suitable for PFALs are 30 cm or shorter in height such as leaf vegetables, transplants, and medicinal plants. Moreover, plants suitable for PFALs should grow well at relatively low light intensity and at high planting density (Kozai and Niu, 2019).

Conforming to these principles, general types of tomato varieties with high plant height are not suitable for cultivation in PFALs during the whole growth period. Dwarf tomato varieties can grow well within a small volume. There are some tomato varieties or cultivars belonging to dwarf tomatoes, such as 'Sweet 'n' Neat', 'Heartbreaker', 'Pot Minibel', 'Tom Thumb', 'Micro-Tom', 'Vilma', 'Balconi Red', 'Yellow Canary' and 'Micro-Gold'. 'Micro-Gold' is a short, compact, and dwarf plant. It is slightly wider and less prostrate than that the 'Micro-Tom' variety (Scott et al., 1995). As the most famous dwarf tomato variety, 'Micro-Tom' has several representative advantages of

dwarf tomatoes compared to general types of tomato varieties. First is the small size; the plant height of adult 'Micro-Tom' is 15–20 cm (Meissner et al., 1997). Most dwarf tomato varieties are shorter than 40 or 50 cm, and could grow properly in a PFAL with higher space use efficacy compared with general types of tomato varieties. The bottom leaves of general types of tomato varieties cultivated in a PFAL receive insufficient light and have to be removed after aging and it wastes the growth space on the bottom. Secondly, dwarf tomatoes can grow at a high planting density. Thirdly, they have a lower light requirement. In the study by Kato et al. (2011), Cross no. 2 plants (transgenic tomatoes bred by cross breeding line 56B and 'Micro-Tom') were grown at a photosynthetic photon flux density (PPFD) of 400 μmol m^{-2} s^{-1} and the net photosynthetic rate saturated at 500 ppm of CO_2 concentration. The fourth advantage is a shorter life cycle, which allows for harvest within 70–90 days after sowing (Sun et al., 2006). This leads to lower production costs and expedites the tomato production process in PFALs. The fifth advantage is high efficiency in genetic transformation. 'Micro-Tom' could be transformed at frequencies of up to 80% through *Agrobacterium*-mediated transformation of cotyledons (Meissner et al., 1997). In addition, compared with other dwarf cultivar, 'Micro-Tom' is used widely for tomato research and 'Micro-Tom' mutant database 'TOMATOMA' has been established (Shikata and Ezura, 2016). In the future, it is worth expecting that many new cultivars are bred by 'Micro-Tom' or its mutant are cultivated in PFAL.

Improving the yield and quality of tomato fruits by breeding or environmental management could be suitably investigated using a model dwarf tomato cultivar in PFALs. Last but not least, because of its small size, rank canopy and colorful fruits, dwarf tomatoes could have ornamental value (de Moraes et al., 2005). Since the dwarf tomatoes have many advantages, they could be cultivated in PFALs to cater to new and growing demands for tomato production.

1.2. Radition-use efficacy (RUE)

In a lettuce PFAL, more than half of the electric power is used for lighting (Ohyama et al., 2002; Graamans et al., 2018). Fruit vegetables such as tomatoes have longer growth cycles and lower harvest indices than leafy vegetables such as lettuce. For example, there are 17–18 days in the cultivation process except 20 days seedling and nursing processes in a nearly 40-day growth cycle of lettuce (Thinh et al., 2019). Moreover, there are about 66 days in the cultivation process except 24 days seedling and nursing processes in a nearly 90-day growth cycle of dwarf tomato (Yano et al., 2006). A lower harvest index indicates that more dry mass production is required for the same yield. Therefore, more energy and electricity are required in a PFAL to produce tomatoes with yield equivalent to leafy vegetables. A significant reduction in electricity cost can be achieved by improving radiation-use efficacy (RUE).

1.2.1. Definition

RUE is regarded as a multi-definitional term. At the leaf level, RUE is often defined as the ratio of CO_2 assimilation to absorbed photons. At the crop level, RUE can be defined as the ratio of dry matter production to absorbed photons, intercepted radiation or incident radiation (Li, 2015). There are two important questions on how to determine the definition of RUE in the calculation.

One is whether the unit of RUE is ‘g MJ^{-1}’ or ‘g mol^{-1}’. The core of RUE is the conversion of solar radiation energy into stored biomass chemical energy. Plants only use solar radiation to synthesize biomass by photosynthesis. Nevertheless, RUE is still a good parameter for light utilization of plants and is used by some simple plant growth models to simulate yield production (Kimball et al., 2002). In filed or greenhouse production systems where solar radiation was utilized, many previous studies used W m^{-2} as the unit of solar radiation (Scholberg et al., 2000; Kleinhenz et al., 2006; Higashide and Heuvelink, 2009; Higashide et al., 2017). Thus, it is straightforward to calculate the intercepted radiation or incident radiation with ‘J’ (Joule) and further

convert it to ‘MJ’. In addition, solar radiation provides not only light but also heat, and energy necessary for crops. However, radiation or light within the wavelength range of 400 to 700 nm (photosynthetic active radiation, PAR) from lamps is utilized mainly for photosynthesis. Fixation of one CO_2 molecule during photosynthesis necessitates eight (or more) photons. Therefore, the quantum number of PAR is an essential factor that can affect the conversion of solar radiation into stored biomass. This is the reason why g mol^{-1} is used as the unit of RUE in this thesis.

The second question is whether RUE is the ratio of dry matter production to intercepted or incident radiation. Some studies conducted in PFALs used g mol^{-1} as the unit of RUE or light-use efficiency (LUE) and calculated it based on the sum of PAR on the cultivation area irradiated by lamps; these studies focused on production efficiency rather than physiological mechanisms (Furuyama et al., 2017; Xu et al., 2021; Liu et al., 2019; Rihan et al., 2020; Larsen et al., 2020). Recently, a few studies determined RUE or LUE based on the cumulative incident radiation on projected leaf area (PLA) (Legendre and van Iersel, 2021; Jayalath and van Iersel, 2021; Jin et al., 2020). Certainly, intercepted radiation is nearly equal to incident radiation when leaf area index (LAI) is large enough or most of the incident radiation is absorbed by plants. When LAI is small, a part of incident radiation is irradiated on the cultivation board and not absorbed by the plant. This leads to an underestimation of RUE. In this thesis, RUE is defined as the ratio of accumulated total dry mass to the amount of PAR received by the canopy in the unit of g mol^{-1}, and the amount of PAR is calculated based on the PLA.

Higher RUE in the modern greenhouse is attributed to a decrease in light extinction coefficient. The value of light extinction coefficient is a parameter that describes the efficiency of light interception in a given canopy (Monsi and Saeki 1953). The high RUE also leads to an increase in leaf photosynthetic rate in modern cultivars, and a more suitable environment (Higashide and Heuvelink, 2009). RUE of tomatoes seems to be higher in PFALs than that in the field and greenhouses (Table 1.1).

Table 1.1. Comparison of different RUE calculation methods and RUE of tomatoes in different production systems.

Production system	Light source	Cultivar or variety	Incident or intercepted radiation	RUE_1 (g MJ^{-1})	RUE_2 (g mol^{-1})	Source
Field	Sun	Agriset 761 and Sunny	Intercepted radiation	2.1	0.46	Scholberg et al., 2000
		Brigade		2.4	0.52	Cavero et al., 1998
Greenhouse		Gourmet and Momotaro York		2.5~3.3	0.54~0.72	Higashide et al., 2017
		Moneymaker, Premier, Extase, Sonatine, Calypso, Liberto, Gourmet, Encore and Momotaro Fight		2.4~3.5	0.52~0.76	Higashide and Heuvelink, 2009
		King Kong 2		2.6	0.57	Kleinhenz et al., 2006
PFAL	Fluorescent lamp	Momotaro	Incident radiation	~5	-	Yokoi et al., 2003
	Metal highlight lamp	Momotaro		-	0.39	Goto, 2012
	LED lamp	Zhezhan No.1 and Dongfeng No.1		~1.3	-	Zheng et al., 2021

The approximation (1 W m^{-2} PAR solar radiation= 4.6 μmol m^{-2} s^{-1} PPFD) comes from the Plant Growth Chamber Handbook (Sager and McFarlane, 1997). RUE_1 is the RUE with the unit of g MJ^{-1}. RUE_2 is the RUE with the unit of g mol^{-1}. The conversion factor from dry mass to chemical energy fixed in dry matter is about 20 MJ kg^{-1} (Kozai, 2013).

In addition, many researchers used ‘efficiency’ rather than ‘efficacy’ in RUE. In fact, ‘efficacy’ could be a more precise terminology than ‘efficiency’. The term

'efficiency' is always expressed as a dimensionless term, such as J J^{-1}, whereas 'efficacy' is not. In this thesis, the unit of RUE is g mol^{-1} which is not dimensionless. Therefore, RUE represents 'radiation-use efficacy' rather than 'radiation-use efficiency'.

1.2.2. Effect of photosynthetic photon flux density (PPFD) on RUE

PPFD can influence the RUE of plants by affecting the photosynthetic rate (Jayalath and van Iersel, 2021), stomatal behavior (Knapp and Smith, 1990; O'Carrigan et al., 2014), photosynthate distribution (He et al., 2019), and chlorophyll content (Valladares and Niinemets, 2008). Jayalath and van Iersel (2021) reported that high PPFD decreased RUE by reducing the quantum yield of photosystem II in lettuce from 50 to 425 μmol m^{-2} s^{-1} PPFD. RUE is the highest under a PPFD of 200 μmol m^{-2} s^{-1} in lettuce and under a PPFD of 250 μmol m^{-2} s^{-1} in basil (Pennisi et al., 2020). The optimal PPFD for high RUE varies among crops. To date, there has been no study investigating the effect of PPFD on RUE of dwarf tomatoes under LED light.

1.2.3. Effect of light quality on RUE

Light quality also influences the RUE of plants. McCree (1971) reported that the relative quantum yield of photosynthesis was the highest at red wavelengths (600–700 nm). In addition, tomatoes (*Solanum lycopersicum* L. cv. Early Girl) grown in monochromatic red light produce more dry biomass than those grown under a combination of red and blue lights (Wollaeger and Runkle, 2014). However, some studies in lettuce (Ohashi-Kaneko et al., 2007; Naznin et al., 2019; Chen et al., 2021), cucumber (Hogewoning et al., 2010), wheat (Goins et al., 1997), and rice (Ohashi-Kaneko et al., 2006) indicated that plants have more biomass or higher net photosynthetic rate under a combination of red and blue lights compared with monochromatic red light. Moreover, the effect of light quality on stomatal conductance in tomatoes varies with the genotype (Ouzounis et al., 2016). Such differences suggest that the effects of red and blue lights on plant biomass production and RUE are highly

species- and cultivar-specific (Goto, 2003; Wollaeger and Runkle, 2014).

In addition to red and blue lights, white light has been used widely in research on lettuce (Zhang et al., 2018; Yan et al., 2019), tomato (Lu et al., 2012), wheat (Cope and Bugbee, 2013; Dong et al., 2014), and vanilla (Bello-Bello et al., 2016) over the last 10 years, especially in the last 5 years, because of several advantages. First, the cost of white LED packages is now ~20% of that of red LEDs, which has contributed to the increase in the fraction of white LEDs to more than 60% in some horticultural fixtures (Kusuma et al., 2020). Second, compared with red and blue lights, white light creates a more pleasant working environment and enables an easier visual assessment of plant health (Kim et al., 2005; Nguyen et al., 2021). Lastly, white light contains useful wide wavebands of spectra other than red and blue lights, such as green light, which can increase photosynthesis and carbon assimilation in the lower parts of leaves (Terashima et al., 2009; Smith et al., 2017). Since white LEDs are widely used in PFALs, in my research on light quality, white light and different combinations of red and blue lights were used to determine the suitable light quality for improving RUE. There are also no previous studies investigating the effect of light quality on RUE of dwarf tomatoes under LED light.

1.3. Fruit biomass radiation-use efficacy (FBRUE)

Tomato plants are divided into two main parts: edible (fruits) and inedible (roots, stems, and leaves) parts. Fruit biomass radiation-use efficiency (FBRUE) can be defined as the ratio of the dry mass of a plant's fruits to the number of photosynthetic photons captured by the plant. It is an important index for the commercial production of tomatoes, indicating the distribution of photoassimilates in fruits. Additionally, FBRUE is a bridge linking photosynthesis and production output.

For general cultivars, the FBRUE of tomato was 0.3 g mol^{-1} in NASA's Biomass Production Chamber (Wheeler et al., 2008), 0.2 g mol^{-1} in a closed plant production system (Goto, 2011), and 0.36 g mol^{-1} in the Permanent Astrobase Life-support Artificial Closed Ecosystem (Li et al., 2019) when tomatoes were harvested. Therefore, there is still room for improving FBRUE. However, few studies have been conducted to improve the FBRUE of dwarf tomatoes in PFALs.

PPFD is an important environmental factor affecting RUE and dry matter distribution, further affecting FBRUE. Yan et al. (2018) reported that the dry matter partitioning of tomato (cultivar, 'Ruifen882') fruits under supplementary artificial light (total daily PAR integral of 15.4 mol m^{-2}) was higher than that without supplementary light (total daily PAR integral of 12.4 mol m^{-2}). However, the effects of PPFD on biomass production and its distribution to plant organs are highly cultivar- and growth-stage-specific. Compared to cultivars with large fruits, Dueck et al. (2010) found that supplementary lighting had less effect on cherry tomatoes in commercial crop management. Plant biomass production and yield are related to the source strength and fruit sink strength, respectively (Heuvelink, 1996; Marcelis, 1996). However, no previous study has elucidated the effects of PPFD on the source and fruit sink strengths of dwarf tomatoes in PFALs.

1.4. Research objectives and thesis outline

The purpose of this thesis is to develop a strategy for controlling light conditions of dwarf tomatoes under LED light to improve RUE during vegetative stage and RUE + FBRUE during reproductive growth stage. Three specific objectives are:

(1) To investigate the effect of PPFD on growth and RUE of dwarf tomatoes and to determine the suitable PPFD for improving RUE at the vegetative growth stage.

(2) To investigate the effect of light quality on growth and RUE of dwarf tomatoes and to determine the suitable light quality for improving RUE at the vegetative growth stage.

(3) To investigate the effect of PPFD on RUE and FBRUE of dwarf tomatoes and to determine the suitable PPFD for improving RUE and FBRUE at the reproductive growth stage.

This thesis is composed of four chapters and the contents of each chapter are as follows:

In **Chapter 1**, a general introduction, including the background on dwarf tomatoes, RUE and FBRUE, related studies, and the objectives of this study, are described. This chapter also identifies knowledge gaps and lists objectives for the research conducted in this thesis. **Chapter 2** deals with specific objectives (1) and (2) by performing two experiments. Specific objective (3) is attained in **Chapter 3**. In addition, I also quantitatively investigate the effects of PPFD on source strength, and fruit sink strength of dwarf tomatoes and determine the suitable PPFD for enhancing yield, and fruit quality under LED light at the reproductive growth stage in **Chapter 3**. In **Chapter 4**, the preceding chapters are summarized, together with presentation of some practical points and perspectives for further research.

CHAPTER 2.

Optimization of PPFD and light quality for increasing radiation-use efficacy in dwarf tomato under LED light at the vegetative growth stage

2.1. Introduction

Plant factories with artificial light (PFALs), also called vertical farms, are becoming popular in many countries for the commercial production of vegetables. Generally, the distance between the adjacent vertical cultivation layers in a PFAL with high space utilization efficiency is approximately 40–50 cm. Therefore, 30 cm or less is the suitable plant height (Kozai and Niu, 2019). Dwarf tomatoes have several advantages compared with general tomatoes in terms of their commercial production in a PFAL: small size with adult 'Micro-Tom' (the most famous dwarf tomato cultivar) plant height of 15–20 cm; can grow at high plant densities (Meissner et al., 1997); probably have low light requirements as the net photosynthetic rate (Pn) of Cross no. 2 plants (transgenic tomato bred by cross-breeding line 56B and 'Micro-Tom') was saturated at a photosynthetic photon flux density (PPFD) of 400 μmol m^{-2} s^{-1} and CO_2 concentration of 500 μmol mol^{-1} (Kato et al., 2011); they have a short life cycle, which allows harvesting within 70–90 days after sowing (Sun et al., 2006), which in turn leads to lower production costs and expedites the tomato production process compared with a general tomato cultivar. Owing to these advantages, dwarf tomatoes can be successfully cultivated in PFALs.

In a PFAL, over 50% of the electricity is consumed in lighting (Ohyama et al., 2002; Graamans et al., 2018). Therefore, a more efficient use of light is one approach to reduce electricity costs. Goto (2011) proposed that the production efficiency of plants cultivated in a PFAL can be measured as photoassimilates per unit molar number of photons (g mol^{-1}). The author calculated the values for rice, strawberry, lettuce, and tomato from the experimental data and indicated that the values did not differ significantly among food crops.

Radiation-use efficiency (RUE) is a good index for measuring radiation utilization by plants (Shibles and Weber, 1965; Williams et al., 1965) and an important quantifier of crop production in relation to photosynthesis, as it combines both the amount of radiation captured by the crop and the production of dry matter. PPFD can influence the RUE of plants by affecting the net photosynthetic rate (Jayalath and van Iersel,

2021), stomatal behavior (Knapp and Smith, 1990; O' Carrigan et al., 2014), photosynthate distribution (Onoda et al., 2014; He et al., 2019), and chlorophyll content (Valladares and Niinemets, 2008; Liu et al., 2014). RUE is the highest under a PPFD of 200 μmol m^{-2} s^{-1} in lettuce and under a PPFD of 250 μmol m^{-2} s^{-1} in basil (Pennisi et al., 2020). The optimal PPFD for high RUE among crops is different.

Light quality also influences the RUE of plants. McCree (1971) reported that the relative quantum yield of photosynthesis was the highest at red wavelengths (600–700 nm). In addition, tomatoes (*Solanum lycopersicum* L. cv. Early Girl) grown in monochromatic red light produce more dry biomass than those grown in combinations of red and blue lights (Wollaeger and Runkle, 2014). However, some studies in lettuce (Ohashi-Kaneko et al., 2007; Naznin et al., 2019; Chen et al., 2021), cucumber (Hogewoning et al., 2010), wheat (Goins et al., 1997) and rice (Ohashi-Kaneko et al., 2006) have indicated that plants have more biomass or higher net photosynthetic rate under a combination of red and blue lights compared with monochromatic red light. Moreover, the effect of light quality on stomatal conductance in tomatoes varies with the genotype (Ouzounis et al., 2016). Such differences suggest that the effects of red and blue lights on plant biomass production and RUE are highly species- and cultivar-specific (Goto, 2003; Wollaeger and Runkle, 2014).

In addition to red and blue lights, white light has been used widely in research on lettuce (Zhang et al., 2018; Yan et al., 2019), tomato (Lu et al., 2012), wheat (Cope and Bugbee, 2013; Dong et al., 2014), and vanilla (Bello-Bello et al., 2016) in the last 10 years, especially in the last 5 years, because of several advantages: first, white LED packages are now ~20% of the cost of red LEDs, which has contributed to the increase in the fraction of white LEDs to more than 60% in some horticultural fixtures (Kusuma et al., 2020). Second, compared with red and blue lights, white light creates a more pleasant working environment and enables an easier visual assessment of plant health (Kim et al., 2005; Nguyen et al., 2021). Lastly, white light contains useful wide wavebands of spectra other than red and blue lights, such as green light, which can increase photosynthesis and carbon assimilation in the lower parts of leaves (Terashima

et al., 2009; Smith et al., 2017). Since white LEDs are widely used in PFALs, in this research, white light and combinations of red and blue lights were used to determine the suitable light quality for improving the RUE. There is also no study investigating the effect of light quality on RUE of dwarf tomatoes under LED light.

It is crucial to develop a strategy for controlling light conditions of dwarf tomatoes during the vegetative and reproductive growth stages. The growth of tomato plants is fast during the vegetative growth stage before anthesis (Monte et al., 2013). The number of leaves of determinate tomatoes (i.e., 'Micro-Tom') is fixed during the vegetative growth stage; therefore, it is necessary to improve the leaf optical properties and photosynthetic capacity. In addition, light intensity and quality can affect the flowering of tomatoes, which is the principal determinant in yield (Dieleman and Heuvelink, 1992; Nanya et al., 2012). Good growth at the vegetative stage is a foundation to further increase yield in the reproductive stage, and enhancing vegetative growth while maintaining a high RUE is the key approach for producing more tomatoes under limited energy. Therefore, we performed two experiments in this study (Experiments 1 and 2) to investigate the effects of PPFD and light quality on plant growth and RUE of dwarf tomatoes and to determine the suitable PPFD and light quality for improving the RUE at the vegetative growth stage.

2.2. Materials and methods

2.2.1. Plant material and growth conditions

A dwarf tomato cultivar, 'Micro-Tom' (*Solanum lycopersicum* L.), was used for the experiment. Tomato seeds were sown in a urethane sponge (M-urethane, M Hydroponics Laboratory Co. Inc., Aichi, Japan) and maintained at 25 °C for 3 days in the dark. Seeds germinated on the 3rd day, and then seedlings were cultivated under white LED lamps (LDL40S-N19/21, Panasonic Corporation, Osaka, Japan) in a room with a controlled environment at Matsudo campus, Chiba University. The following conditions were maintained—the PPFD was set to 200 μmol m^{-2} s^{-1} at the canopy level using a quantum sensor (LI-190, LI-COR Inc., Lincoln, NE, USA) and air temperature of 25/20 °C (light/dark period) with 70% relative humidity, 1000 μmol mol^{-1} CO_2 concentration, and 16 h/8 h (light/dark) photoperiod were maintained. All plants were cultivated using 1/2 OAT house A nutrient (OAT Agrio Co., Ltd., Tokyo, Japan) from 7 days after germination. pH and electrical conductivity of the nutrition solution were set at 6.3 and 1.3 dS m^{-1}, respectively. The nutrition solution was renewed every 4 days. Seedlings were grown under these conditions until the third true leaf (from the bottom) fully expanded, which occurred 24 days after sowing, after which the seedlings were transplanted into the treatment area.

2.2.2. Experimental conditions

2.2.2.1. Experiment 1: PPFD effect

Ninety-six uniform seedlings were equally divided and inserted into three polystyrene foam boards placed over 18.6 L containers (600 mm × 300 mm × 141 mm; SANKO Co. Ltd., Tokyo, Japan). Each container was placed under one of the three different PPFDs in a growth chamber with white LED lamps (customized lamp, color temperature: 4000 K; Showa Denko K. K., Tokyo, Japan). The different light treatments were: W300 (PPFD: 300 μmol m^{-2} s^{-1}, daily light integral (DLI): 17.28 mol m^{-2} d^{-1}), W500 (PPFD: 500 μmol m^{-2} s^{-1}, DLI: 28.80 mol m^{-2} d^{-1}), and W700 (PPFD: 700 μmol m^{-2} s^{-1}, DLI: 40.32 mol m^{-2} d^{-1}). The above PPFDs were the average values above the top of the canopies and were chosen based on a previous study (data not shown). The environmental conditions, except for light conditions, were the same as

those before transplanting. The spectral photon flux distribution of the white LED lamp was measured using a spectroradiometer (USR-45DA, USHIO Inc., Tokyo, Japan), as shown in Figure 2.1. The fractions of blue, green, and red wavelengths, as well as red/blue ratio, were calculated (Table 2.1). The planting density of seedlings was 476.2 plant m^{-2}. The side shoots of all plants were pruned when visible. The first flowers of half of the plants bloomed 10 days after treatment (DAT).

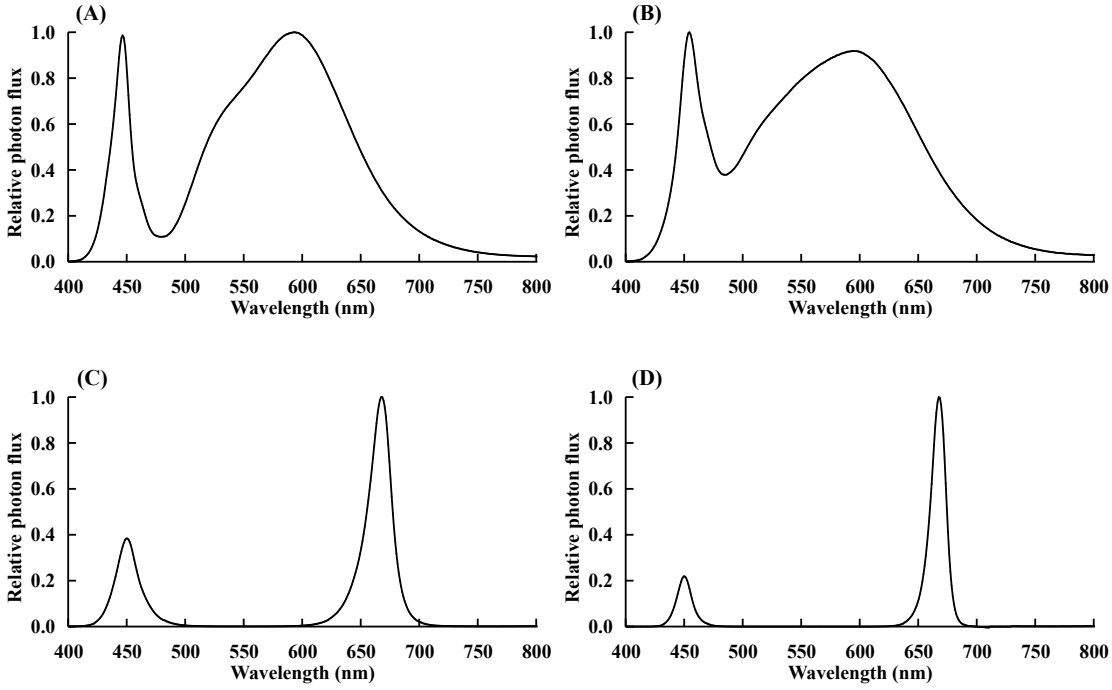

Figure 2.1 Spectral photon flux distributions of white LED lamp (customized lamp) in Experiment 1 (A), white LED lamp (LDL40S-N19/21) in Experiment 2 (B), as well as red and blue LED lamps in R3B1 (C) and R9B1 (D) in Experiment 2. R3B1 and R9B1 represent photon flux ratios (red to blue light) of 3:1 and 9:1, respectively. The peak wavelengths of the white lamp were 446 nm and 592 nm in Experiment 1 and 454 nm and 593 nm in Experiment 2. The peak wavelengths of red and blue light were 667 and 450 nm, respectively, in Experiment 2. The maximum value of photon flux was converted to 1.0.

Table 2.1 Spectral data for LED lamps at the wavelength of 400–700 nm. '%' represents the ratios of blue, green, red, and far-red photon fluxes as a percentage of photon flux density. R/B ratio represents the photon flux ratio of red light to blue light. 'W' represents white LED lamps. R3B1 and R9B1 represent red-blue LED lamps with photon flux ratios of 3:1 and 9:1, respectively, of red to blue light. The phytochrome photostationary state (PSS) is calculated using spectral composition and intensity of light received by plants (Sager et al., 1988; Stutte, 2009).

	W in Experiment 1	**W in Experiment 2**	**R3B1**	**R9B1**
% Blue (400–499 nm)	17.1	21.5	24.5	9.9
% Green (500–599 nm)	46.7	42.9	0.4	0.4
% Red (600–699 nm)	32.9	31.5	74.7	89.0
% Far-red (700–800 nm)	3.3	4.0	0.4	0.7
R/B ratio	1.9	1.5	3.0	9.0
PSS	0.85	0.84	0.87	0.88

2.2.2.2. Experiment 2: light quality effect

Ninety-six uniform seedlings were equally divided into three containers, as in Experiment 1. The three containers were placed in a growth chamber with three different light quality lamps. The spectral photon flux distributions of the white LED lamp (LDL40S-N19/21, Panasonic Corporation, Osaka, Japan) and RB LED lamps (CIVILIGHT, DPT2RB120Q33 40 type, Showa Denko K.K., Tokyo, Japan) are shown in Figure 2.1. The fractions of blue, green, and red wavelength ranges of the lamps are listed in Table 2.1. Different light quality treatments—W (white light) and a mixture of red (R) and blue (B) lights, R3B1 (R:B = 3:1) and R9B1 (R:B = 9:1)—were administered. The PPFD of the three treatments was set at 300 μmol m^{-2} s^{-1} based on the results of Experiment 1. The environmental conditions, except for the light conditions, were the same as in Experiment 1.

2.2.3. Growth measurement

Growth parameters were measured every 2–5 days from 0 to 9 DAT in Experiment 1, to 10 DAT in Experiment 2, respectively. The growth parameters measurement in both experiments were performed with two replicates. Stem length was measured from the main stem base to the top of the stem with a ruler. 'Micro-Tom' is one kind of

determinate tomato. There is no new leaf on the main stem after the first truss. The number of leaves on the main stem, which is also the leaf number until the first truss, was recorded. Eight and nine plants were used in each treatment of Experiments 1 and 2 in two replicates and were sampled destructively for biomass analysis as well as leaf area measurement at the end of the experiments, respectively. Fresh and dry weights of plant organs (leaves, stems, and roots) were determined. Plant organs were dried for 72 h at 80 °C in a convection oven. Leaf area (LA, cm^2) was measured using a leaf area meter (LI-3000C, LI-COR Inc., Lincoln, NE, USA). Specific leaf area (SLA, $cm^2\ g^{-1}$) was calculated by dividing LA (cm^2) by the dry leaf weight (g).

2.2.4. RUE of canopy

Understanding the basic determinants of RUE is vital for enhancing the productivity and energy use efficiency of dwarf tomatoes in PFALs. It is necessary to carefully use the RUE definitions in PFALs. Some studies used g mol^{-1} as the unit of RUE and calculated it based on the sum of PAR on the cultivation area or irradiation by lamps, which focused on the production efficiency rather than the physiological mechanisms (Liu et al., 2019; Rihan et al., 2020; Xu et al., 2021). Recently, a few studies have defined RUE based on the cumulative incident radiation on the PLA (Jayalath and van Iersel, 2021; Jin et al., 2020; Legendre and van Iersel., 2021). Certainly, the intercepted radiation is nearly equal to the incident radiation when the LAI is sufficiently large, or almost all the incident radiation is absorbed by the plant. When the LAI is small, a part of the incident radiation is irradiated on the cultivation surface and is not absorbed by the plant. Therefore, we chose the latter method in this study.

RUE (g mol^{-1}) is defined as the proportion of the accumulated total dry mass to the integrated PPFD received by the plant during a given period.

$$RUE = \frac{\Delta W}{\Delta I_{PPFD}} \tag{2-1}$$

where ΔW (g) is the accumulated total dry mass during a period, and ΔI_{PPFD} (mol) is the integrated PPFD received by the plant during a given period (from 3 to 9 DAT in Experiment 1 and from 3 to 10 DAT in Experiment 2, respectively).

ΔW (g) during a given period ($t_1 - t_0$) is defined as follows:

$$\Delta W = W_{t_1} - W_{t_0} \ (t_0 < t_1) \quad (2\text{-}2)$$

where W_{t_0} (g) and W_{t_1} (g) are the total dry mass of the plant on the first day (t_0) and the last day (t_1) of a given period, respectively.

The ΔI_{PPFD} (mol) during a given period ($t_1 - t_0$) was calculated as follows:

$$\Delta I_{PPFD} = a \times \sum_{t=t_0}^{t_1} [PLA(t) \times (PPFD_T - PPFD(t))] \ (t_0 < t \leq t_1) \quad (2\text{-}3)$$

where 'a' is the conversion factor for the light period of 1 day—5.76×10^4 s (16 h × 3600 s h^{-1}). *PLA(t)* is the *PLA* (m^2) of the plant on day *t*. $PPFD_T$ is the PPFD at the top of the canopy (mol m^{-2} s^{-1}), and it is specific for each treatment. *PPFD(t)* is the PPFD (mol m^{-2} s^{-1}) at the bottom of the canopy on day *t*.

The PPFDs above the top of the canopies were measured every day using a quantum sensor (LI-190, LI-COR Inc., Lincoln, NE, USA) and GaAsp photodiodes (G1118, Hamamatsu Photonics K. K., Shizuoka, Japan), and maintained at 300, 500, and 700 μmol m^{-2} s^{-1} in W300, W500, and W700 in Experiment 1, respectively. PPFDs of 69–86 evenly distributed points on the bottom of the canopy and on the surface of the polystyrene foam board were measured with the quantum sensor from 3 to 9 DAT. PPFDs of 40–50 evenly distributed points above the top of the canopy were measured with the GaAsp photodiodes. In contrast, PPFDs above the top of canopies in Experiment 2 were maintained at 300 μmol m^{-2} s^{-1} in all cases. PPFDs of 43–80 measurement points on the canopy bottom were measured with the quantum sensor every day from 3 to 10 DAT. The intercepted PPFD of the canopy was calculated as the difference between the average PPFD above the top and on the bottom of the canopy. The intercepted PPFD proportion was calculated as the ratio of the intercepted PPFD to the average PPFD above the top of the canopy.

Photographs of the canopy were taken from the top every day, and PLA per plant (Furuyama et al., 2017) was determined from the photographs using a free imaging software (LIA 32 ver. 0.378, Yamamoto) from 1 to 9 DAT in Experiment 1 and from 2 to 10 DAT in Experiment 2.

The photosynthetic quantum yield (ϕ, mmol CO_2/mol photon) is defined as RUE directly at the leaf level and can reflect the RUE of the canopy in this study. The ϕ was calculated as the ratio of the Pn to PPFD.

2.2.5. Leaf optical properties and chlorophyll concentration

The reflection and transmission spectra of the third leaf (fully expanded and unshaded leaf) from the top of the plant were measured using a spectrophotometer (V-750, JASCO Corporation, Tokyo, Japan) with an integrating sphere unit (ISV-922, JASCO Corporation, Tokyo, Japan) at 10 DAT. The range of the measured light spectrum was 400–700 nm. Eight and four plants in each treatment in Experiments 1 and 2 were sampled, respectively. Absorptance was calculated for each wavelength as follows:

$$\text{Absorptance} = 100\% - (\text{Reflectance} + \text{Transmittance}) \quad (2\text{-}4)$$

Chlorophyll pigment was extracted from the third leaf from the top of the plant with N,N-dimethylformamide at 10 DAT, according to the protocol described by Porra et al. (1989). For chlorophyll concentration analysis, four leaves from four plants in each treatment were sampled. The chlorophyll concentration was determined on a dry weight basis by measuring the absorbance of the leaf extracts at 663.8, 646.8, and 750.0 nm using an ultraviolet-visible spectrophotometer (V-750, JASCO Corporation, Tokyo, Japan).

2.2.6. Gas exchange

The Pn was determined for the third leaf of four randomly selected plants in each treatment at 10 DAT using a portable photosynthesis measurement system (LI-6400XT, LI-COR Inc., Lincoln, NE, USA), equipped with a transparent cuvette under the following environmental conditions: 25 ± 1 °C leaf temperature, 65–70% relative humidity, and 1000 μmol mol^{-1} CO_2 concentration. The leaves were clamped into the cuvette until the Pn and stomatal conductance were stable at every measurement. The flow rate of air through the system was set to 500 μmol s^{-1}.

The response of Pn to PPFD was also determined on the third leaf in each treatment using the LI-6400XT photosynthesis measurement system, equipped with a 6400-02B LED light source (90% red light with peak at 665 nm, and 10% blue light with peak at 470 nm) in a leaf chamber. The leaves were clamped into the cuvette at 1000 μmol m^{-2} s^{-1} PPFD until the Pn and stomatal conductance were stable. The following PPFD gradient was set at the leaf surface—2000, 1500, 1000, 800, 500, 300, 200, 100, 50, and 0 μmol m^{-2} s^{-1}. Leaf temperature, relative humidity, and CO_2

concentration were set at 25 ± 1 °C, 65–70%, and 1000 μmol mol^{-1}, respectively. The flow rate of air through the system was set to 500 μmol s^{-1}.

2.2.7. Statistical analysis

Data were statistically evaluated by one-way analysis of variance (ANOVA) using the SPSS program for Windows (Version 24.0; SPSS Inc., Chicago, IL, USA). To investigate significant differences among the treatments, the mean value of the measured data was compared using the Tukey−Kramer test at $p < 0.05$.

2.3. Results

2.3.1. Experiment 1: PPFD effect

2.3.1.1. Growth characteristics

The total fresh and dry weights, LA, and SLA were significantly affected by PPFD (Table 2.2). Seedlings under 700 μmol m^{-2} s^{-1} PPFD had the highest LA, and fresh and dry weights. SLA of plants was significantly higher under 300 μmol m^{-2} s^{-1} of PPFD compared with that under 500 and 700 μmol m^{-2} s^{-1}. However, PPFD had no significant effect on the stem length. Furthermore, no significant differences were found in leaf number and dry matter ratio among the treatments.

Table 2.2 Effect of photosynthetic photon flux density (PPFD) on the growth of 'Micro-Tom' 9 days after treatment (DAT) in Experiment 1. W300, W500, and W700 denote PPFD of 300, 500, and 700 μmol m^{-2} s^{-1}, respectively. Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on the Tukey−Kramer's test (n = 8) at $p < 0.05$.

Treatment	Stem Length (cm)	Leaf Number	Total Fresh Weight (g)	Total Dry Weight (g)	Dry Matter Ratio (%)	Leaf Area (cm^2)	Specific Leaf Area (cm^2 g^{-1})
0 DAT	2.4 ± 0.1	3.5 ± 0.2	0.50 ± 0.03	0.05 ± 0.00	9.81 ± 0.20	-	-
W300	3.4 ± 0.2	6.6 ± 0.2	5.69 ± 0.54 c	0.50 ± 0.04 c	8.81 ± 0.15	73.46 ± 4.18 b	257.60 ± 14.92 a
W500	3.8 ± 0.1	6.6 ± 0.2	7.71 ± 0.60 b	0.73 ± 0.06 b	9.55 ± 0.15	83.66 ± 2.33 b	199.68 ± 20.14 b
W700	3.8 ± 0.2	6.4 ± 0.2	9.55 ± 0.33 a	0.92 ± 0.05 a	9.57 ± 0.30	95.50 ± 2.01 a	167.96 ± 9.10 b

2.3.1.2. Light interception and RUE

The increase in the PLA was similar among the three treatments (Figure S2.1). The daily averages of the intercepted PPFD proportions of the canopy in W300, W500, and W700 were 0.89, 0.88, and 0.87, respectively (Table 2.3). The intercepted PPFD increased with time for all treatments (Figure S2.2a), and the intercepted PPFD proportions exceeded 0.90 from 7 DAT (Figure S2.2b). The ΔW from 3 to 9 DAT in W300, W500, and W700 were 0.34, 0.56, and 0.62 g, respectively (Table 2.2). RUE (Table 2.3) and ϕ (Table 2.4) increased with the decrease in PPFD and were the highest for W300 among the three treatments. The intercepted PPFD proportions exceeded 0.90 when the LAI was greater than three (Figure S2.3).

Table 2.3 Effects of PPFD on light interception, biomass production, and radiation-use efficiency (RUE) of 'Micro-Tom' during the 6-day experimental period in Experiment 1. ΔW (g) is the accumulated total dry mass during the experimental period. RUE is defined as the ratio of the accumulated total dry mass to integrated PPFD received by the plant during the period. W300, W500, and W700 denote 300, 500, and 700 μmol m^{-2} s^{-1} PPFD, respectively. Each value of ΔW represents the average of four plants.

Treatment	Integrated PPFD Received by the Plant during the Period (mol)	Daily Average Intercepted PPFD Proportion during the Period	ΔW (g)	RUE (g mol^{-1})
W300	0.30	0.89	0.34	1.15
W500	0.49	0.88	0.56	1.14
W700	0.66	0.87	0.62	0.94

Table 2.4 Effect of PPFD on the photosynthetic quantum yield (ϕ) of leaves in 'Micro-Tom' 10 DAT in Experiment 1. ϕ is the ratio of net photosynthetic rate to PPFD (mmol CO_2/mol photon). Each value represents the mean ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ ($n = 4$). W300, W500, and W700 denote 300, 500, and 700 μmol m^{-2} s^{-1} PPFD, respectively.

Treatment	ϕ (mmol CO_2/mol Photon)
W300	40.82 ± 0.57 a
W500	39.38 ± 0.36 a
W700	34.31 ± 0.67 b

2.3.1.3. Leaf optical properties and chlorophyll concentration

Top leaves under higher PPFDs (W500 and W700) reflected significantly more PAR than those in W300 (Table 2.5 and Figure 2.2). The transmittance of leaves under green light (500–599 nm) in W300 was significantly higher than that in W700 (Table 2.5). PPFD mostly affected the optical characteristics of the leaves in green light (Figure 2.2).

Table 2.5 Effects of PPFD on the transmittance and reflectance of leaves in 'Micro-Tom' at blue, green, and red wavelengths 10 DAT in Experiment 1. The range of measured light spectrum was 400–700 nm. Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on the Tukey−Kramer's test at $p < 0.05$ ($n = 8$). W300, W500, and W700 denote 300, 500, and 700 µmol m^{-2} s^{-1} PPFD, respectively.

Treatment	Transmittance (%)			Reflectance (%)		
	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)
W300	0.5 ± 0.1	7.3 ± 0.7 a	3.4 ± 0.4	5.0 ± 0.1 b	7.1 ± 0.3 b	5.2 ± 0.1 b
W500	0.3 ± 0.1	5.6 ± 0.5 ab	2.7 ± 0.4	5.8 ± 0.1 a	8.5 ± 0.2 a	6.3 ± 0.1 a
W700	0.3 ± 0.0	5.1 ± 0.5 b	2.5 ± 0.3	6.0 ± 0.3 a	9.7 ± 0.5 a	6.9 ± 0.3 a

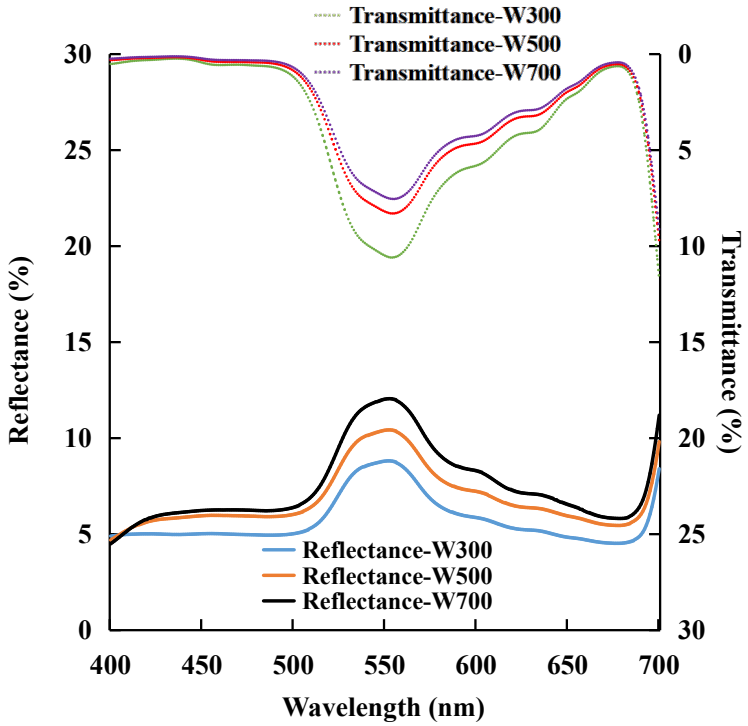

Figure 2.2 Effects of PPFD on the spectra of reflectance and transmittance of leaves in 'Micro-Tom' 10 DAT in Experiment 1. The range of measured light spectrum was 400–700 nm. W300, W500, and W700 denote 300, 500, and 700 µmol m^{-2} s^{-1} PPFD, respectively. Each value represents the average of the values of eight plants.

Chlorophyll concentration decreased as PPFD increased (Table 2.6). Chlorophyll concentration was the lowest in W700; moreover, the concentrations of both

chlorophyll a and b decreased with the increase in PPFD. PPFD had no significant effect on chlorophyll a/b ratio.

Table 2.6 Effect of PPFD on chlorophyll concentration (conc.) of leaves in 'Micro-Tom' 10 DAT in Experiment 1. DW (g) is dry weight. Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on Tukey−Kramer's test at the $p < 0.05$ ($n = 4$). W300, W500, and W700 denote 300, 500, and 700 µmol m^{-2} s^{-1} PPFD, respectively.

Treatment	Chlorophyll a Conc. (mg g^{-1} DW)	Chlorophyll b Conc. (mg g^{-1} DW)	Chlorophyll a + b Conc. (mg g^{-1} DW)	Chlorophyll a/b
W300	20.7 ± 2.0 a	5.9 ± 0.4 a	26.6 ± 2.4 a	3.5 ± 0.2
W500	16.7 ± 0.6 ab	4.6 ± 0.2 b	21.3 ± 0.8 a	3.6 ± 0.1
W700	12.5 ± 0.2 b	3.4 ± 0.0 c	15.9 ± 0.2 b	3.7 ± 0.0

2.3.1.4. Net photosynthetic rate (Pn) and light response

Pn differed significantly among the leaves of seedlings grown under different PPFD treatments (Figure 2.3). Increasing the PPFD from 300 to 700 µmol m^{-2} s^{-1} resulted in a significant increase in Pn from 12.2 to 24.0 µmol CO_2 m^{-2} s^{-1}, with the highest Pn obtained at a PPFD of 700 µmol m^{-2} s^{-1}.

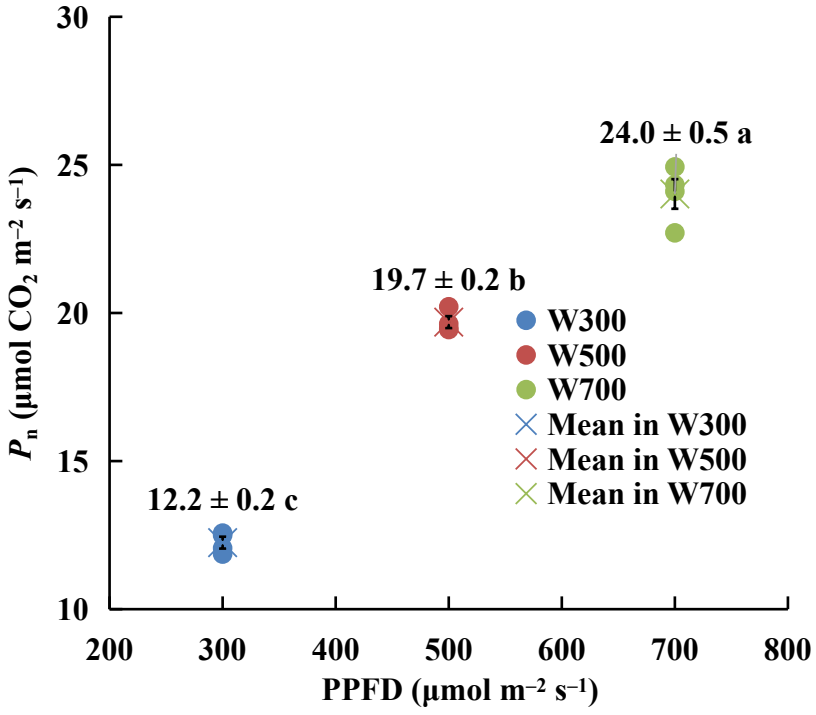

Figure 2.3 Effect of PPFD on net photosynthetic rate (Pn) of leaves in 'Micro-Tom' 10 DAT in Experiment 1. Four plants were measured for each PPFD. Solid point denotes the measured value for one plant. X-mark represents the average Pn of four plants in each treatment. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey–Kramer's test at $p < 0.05$ (n = 4). W300, W500, and W700 denote 300, 500, and 700 µmol m^{-2} s^{-1} PPFD, respectively.

The Pn of the third leaf increased rapidly as PPFD increased to 500 µmol m^{-2} s^{-1} and then increased slowly to a maximum in all treatments (Figure 2.4). The Pn measured at PPFDs of 50, 100, and 2000 µmol m^{-2} s^{-1} in W700 were significantly lower than those in W300.

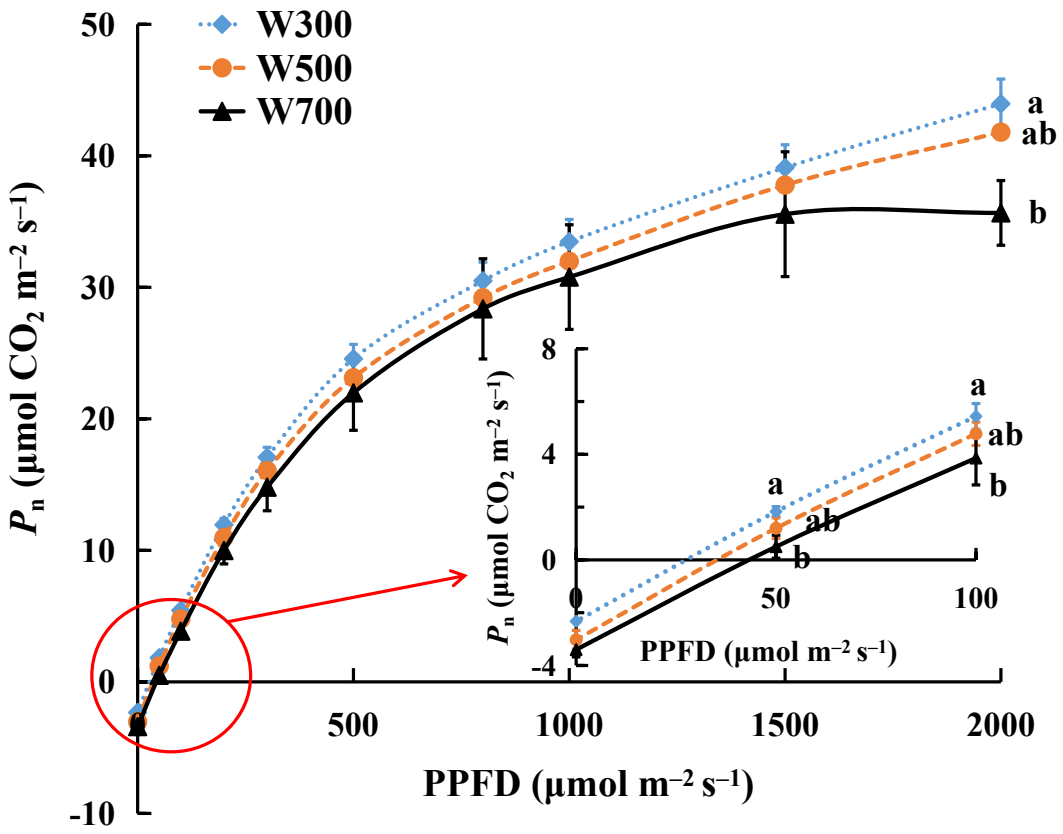

Figure 2.4 Light response curve of net leaf photosynthetic rate in 'Micro-Tom' 11 DAT in Experiment 1. The Pn to PPFD was determined on the third leaf (counted from top, fully expanded, and unshaded leaf). Each value represents the average of three plants. Error bars represent ± standard error. Different letters indicate significant differences

among the treatments based on Tukey−Kramer's test at $p < 0.05$. W300, W500, and W700 denote PPFDs of 300, 500, and 700 μmol m^{-2} s^{-1}, respectively.

2.3.2. Experiment 2: light quality effect

2.3.2.1. Growth characteristics

Light quality had a significant impact on the stem length, dry weight, dry matter ratio, and SLA (Table 2.7). The stem length under R3B1 was significantly lower than under W and R9B1. The dry weight and dry matter ratio under R9B1 were significantly higher than those under R3B1. Plants under R9B1 had the lowest SLA. There were no significant differences in leaf number, fresh weight, and LA among the three treatments.

Table 2.7 Effect of light quality on the growth of 'Micro-Tom' 10 DAT in Experiment 2. Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ ($n = 9$). W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

Treatment	Stem Length (cm)	Leaf Number	Total Fresh Weight (g)	Total Dry Weight (g)	Dry Matter Ratio (%)	Leaf Area (cm^2)	Specific Leaf Area (cm^2 g^{-1})
0 DAT	3.5 ± 0.3	3.4 ± 0.1	0.55 ± 0.03	0.06 ± 0.00	10.92 ± 0.41	-	-
W	4.7 ± 0.1 a	6.4 ± 0.2	7.93 ± 0.46	0.66 ± 0.04 ab	8.34 ± 0.12 b	130.60 ± 4.12	313.59 ± 6.91 a
R3B1	4.4 ± 0.0 b	6.4 ± 0.2	7.10 ± 0.39	0.59 ± 0.03 b	8.33 ± 0.21 b	115.13 ± 5.91	308.03 ± 6.07 a
R9B1	4.8 ± 0.1 a	6.0 ± 0.0	7.90 ± 0.27	0.71 ± 0.03 a	9.00 ± 0.52 a	130.36 ± 4.79	281.91 ± 4.51 b

2.3.2.2. Light interception and RUE

The PLA of plants under R3B1 was the lowest from 8 to 10 DAT among the three treatments (Figure S2.4). The daily average of intercepted PPFD proportions of the canopy in W, R3B1, and R9B1 were 0.92 (Table 2.8). The intercepted PPFD increased with time for all treatments (Figure 2.5), and the intercepted PPFD proportions exceeded 0.90 from 6 DAT. The ΔW in W, R3B1, and R9B1 were 0.50, 0.46, and 0.56 g, respectively, from 3 to 10 DAT. The RUE of plants under R9B1 was the highest among the three treatments, being 1.18-fold higher than that under R3B1 (Table 2.8). Nevertheless, the RUE in R3B1 was almost the same as that in W. The lowest fraction of blue light (R9B1) led to the highest ϕ (Table 2.9). The intercepted PPFD proportions exceeded 0.90 when LAI was greater than three (Figure S2.5).

Table 2.8 Effects of light quality on light interception, biomass production, and RUE of 'Micro-Tom' during the 7-day experimental period in Experiment 2. ΔW (g) is the total dry mass accumulated during the experimental period. Each value of ΔW represents the average of six plants. RUE (g mol^{-1}) is defined as the ratio of the accumulated total dry mass to integrated PPFD received by the plant during the experimental period. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

Treatment	Integrated PPFD Received by the Plant during the Period (mol)	Daily Average Intercepted PPFD Proportion during the Period	ΔW (g)	RUE (g mol^{-1})
W	0.43	0.92	0.50	1.15
R3B1	0.40	0.92	0.46	1.13
R9B1	0.42	0.92	0.56	1.36

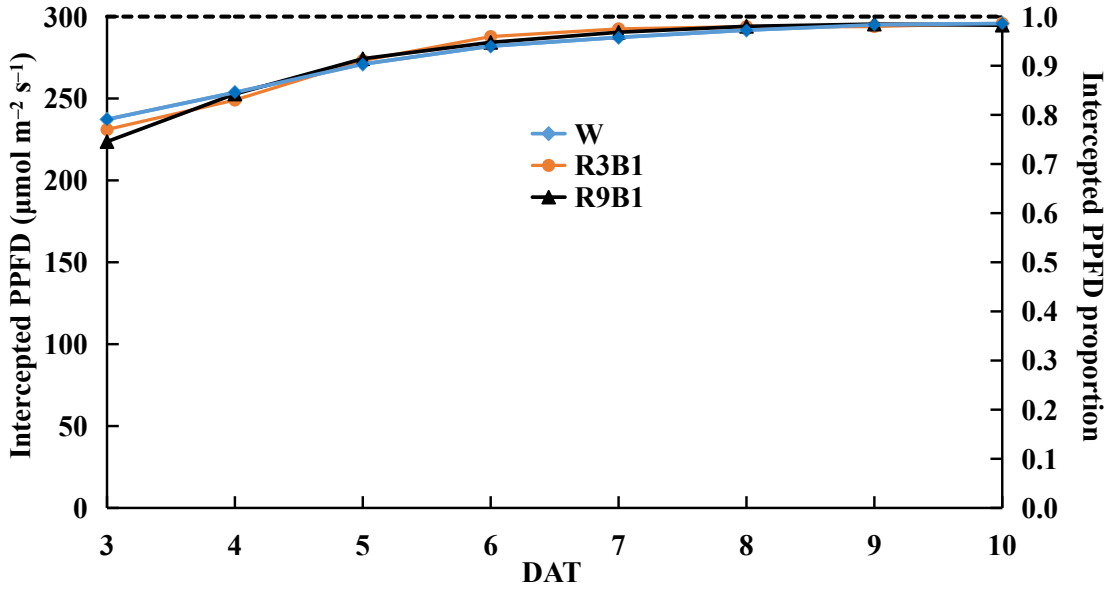

Figure 2.5 Effects of light quality on daily average of intercepted PPFD and proportion of the canopy in 'Micro-Tom' in Experiment 2. The intercepted PPFD of the canopy was calculated as the difference between the average PPFD on the top and bottom of the canopy. The intercepted PPFD proportion was calculated as the ratio of the intercepted PPFD to the average PPFD above the top of the canopy. The PPFD of the three treatments was set at 300 µmol m^{-2} s^{-1}. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

Table 2.9 Effect of light quality on the ϕ of leaves in 'Micro-Tom' 10 DAT in Experiment 2. ϕ is the ratio of net photosynthetic rate to PPFD and expressed in mmol CO_2/mol photon. Each value represents the mean ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at the $p < 0.05$ ($n = 4$). W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

Treatment	ϕ (mmol CO_2/mol Photon)
W	35.05 ± 1.62 ab
R3B1	32.39 ± 0.70 b
R9B1	38.72 ± 0.54 a

2.3.2.3. Leaf optical properties and chlorophyll concentration

The leaves could reflect more green light under R9B1 than under W in Experiment 2 (Table 2.10 and Figure S2.6). The reflectance of the leaves was the lowest under W. There were no significant differences in the transmittance among the three treatments (Figure S2.6).

Table 2.10 Effect of light quality on the reflectance of leaves in 'Micro-Tom' at blue, green, and red wavelengths 10 DAT in Experiment 2. The range of the measured light spectrum was 400–700 nm. Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ ($n = 4$). The PPFD of treatments was set at 300 μmol m^{-2} s^{-1}. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

Treatment	Reflectance (%)		
	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)
W	5.1 ± 0.3	7.4 ± 0.2 b	5.3 ± 0.1
R3B1	5.6 ± 0.1	7.8 ± 0.2 ab	5.7 ± 0.2
R9B1	5.3 ± 0.1	8.4 ± 0.3 a	5.7 ± 0.2

The concentration of chlorophyll decreased significantly with an increase in the R/B light ratio (Table 2.11). The chlorophyll concentration under W was significantly higher than that under R9B1. However, light quality had no significant effect on the chlorophyll a/b ratio.

Table 2.11 Effect of light quality on chlorophyll concentration (conc.) of leaves in 'Micro-Tom' 10 DAT in Experiment 2. DW (g) is dry weight. Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ ($n = 4$). The PPFD of three treatments was set at 300 μmol m^{-2} s^{-1}. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

Treatment	Chlorophyll a Conc. (mg g^{-1} DW)	Chlorophyll b Conc. (mg g^{-1} DW)	Chlorophyll a + b Conc. (mg g^{-1} DW)	Chlorophyll a/b
W	22.9 ± 1.2 a	7.3 ± 0.5 a	30.1 ± 1.5 a	3.2 ± 0.1
R3B1	19.6 ± 0.6 ab	6.1 ± 0.2 ab	25.7 ± 0.7 ab	3.2 ± 0.0
R9B1	16.9 ± 0.5 b	5.2 ± 0.2 b	22.1 ± 0.6 b	3.2 ± 0.0

2.3.2.4. Pn and light response

Pn differed significantly among the leaves grown under different proportions of R and B lights (Figure 2.6). The Pn of leaves under R9B1 (11.6 μmol CO_2 m^{-2} s^{-1}) was significantly higher than that under R3B1 (9.7 μmol CO_2 m^{-2} s^{-1}).

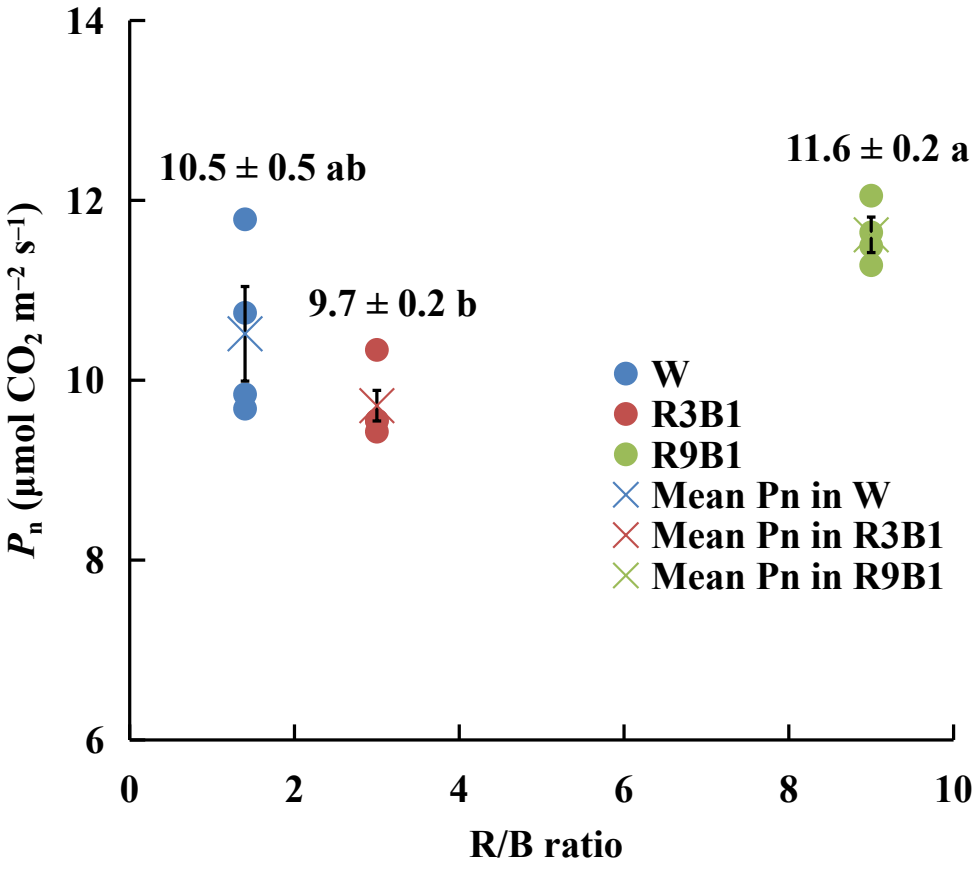

Figure 2.6 Effect of light quality on Pn of leaves in 'Micro-Tom' 10 DAT in Experiment 2. Four plants were measured for each PPFD. Solid point denotes the measured value for one plant. X-mark represents the average Pn of four plants in each treatment. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey–Kramer's test at $p < 0.05$ ($n = 4$). W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

The Pn of the third leaf increased rapidly as PPFD increased to 500 μmol m^{-2} s^{-1} and then increased slowly to a maximum in all treatments (Figure S2.7). At a PPFD of 2000 μmol m^{-2} s^{-1}, Pn under W was significantly lower than that under R9B1 and R3B1. However, there were no significant differences in Pn at other values of PPFD.

2.4. Discussion

2.4.1. Experiment 1: PPFD effect

Experiment 1 demonstrated that PPFD had significant effects on total fresh and dry weights, LA, and SLA (Table 2.2). Generally, plants have long stems, resulting in tall plants, to promote light capture under shade conditions (Gommers et al., 2013; Park and Runkle, 2017). Some studies conducted in PFALs or growth chambers with artificial light indicated that stem elongation decreased with an increase in PPFD (Feng et al., 2019; Jones-Baumgardt et al., 2019). However, other studies have reported that high PPFD results in long stems, thereby increasing the plant height (Ma et al., 2010; Yao et al., 2017). In the case of tomatoes, the plant height of the cherry tomato seedlings (*Solanum lycopersicum* cv. Mill qianxi) decreased when PPFD increased from 50 to 500 μmol m^{-2} s^{-1} (Fan et al., 2013). A similar result was demonstrated in a study by Matsuda et al. (2016), in which the stem length of the tomato cultivar 'Momotaro Fight' was significantly longer at a PPFD of 150 μmol m^{-2} s^{-1} than that of 300 μmol m^{-2} s^{-1}. Another study by He et al. (2019) used the 'Mill qianxi' tomato cultivar and found that plant height increased when PPFD was increased from 50 to 300 μmol m^{-2} s^{-1} but decreased when PPFD was further increased to 550 μmol m^{-2} s^{-1}. The stem lengths of different species and cultivars might respond differently to PPFD under different experimental conditions. In Experiment 1, there was no significant difference in the stem length of plants under different PPFD treatments, probably because the cultivar 'Micro-Tom' is a dwarf tomato. Experiment 1 verified that higher PPFD leads to lower LA (Figure S2.8) and SLA (Fan et al., 2013) (PPFD: 50–550 μmol m^{-2} s^{-1}), and higher fresh and dry weights (Larsen et al., 2020) (PPFD: 50–600 μmol m^{-2} s^{-1}) of plants under LED light (Table 2.2).

The ratio of PAR above the top of the canopy in W300, W500, and W700 was 3:5:7. The ratio of average PAR received by one plant in the three treatments was 3.0:4.9:6.6 (Table 2.3). However, the ratio of dry mass produced by one plant during the period was close to 3.0:4.8:5.5, which differed from the 3.0:4.9:6.6 ratio. The plants under W700 intercepted a lower proportion of PPFD and produced less dry mass per mole PAR photons than those under W300 and W500 during the 6-day experimental period. In addition, PPFD increased Pn (Figure 2.3) but reduced ϕ (Table 2.4). Jayalath and van Iersel (2021) also reported that a high PPFD decreased the RUE by reducing

the quantum yield of photosystem II. In Experiment 1, the RUE of plants in W300 was the highest among the three treatments. Therefore, 300 μmol m^{-2} s^{-1} was selected as the proper value of PPFD above the top of the canopy for 'Micro-Tom' cultivation at the vegetative growth stage to enhance the RUE.

In natural conditions, light is one of the limiting resources, and plants grown under low PPFD must adapt to capture light efficiently (Lee and Graham, 1986). In contrast, leaves under high PPFD conditions have thicker cuticles and lower SLA and chlorophyll concentrations than those grown under low PPFD conditions (Araus and Hogan, 1994; Sanches and Válio, 2006). These characteristics increase the reflectance of leaves (Sanches and Válio, 2006; Tanner and Eller, 1986), which may explain the higher reflectance and lower transmittance (lower absorptance) of leaves under high PPFD than those under low PPFD (Table 2.5 and Figure 2.2). In addition, lower leaves shared more light because of the significantly low reflectance and absorptance of the top-layer leaves at low PPFD, and might have a more uniform vertical PPFD distribution, which could contribute to the canopy RUE (Li et al., 2014). He et al. (2019) reported that leaf chlorophyll concentration in tomatoes increased with a decrease in PPFD within a certain range (300–550 μmol m^{-2} s^{-1}). To capture more light under a low PPFD, leaves must distribute more dry mass to produce more chlorophyll. Under excessive or long-term high PPFD, chlorophyll could be damaged or destroyed, resulting in a low chlorophyll concentration (Table 2.6).

Usually, leaves have lower net photosynthetic rates at high PPFD but higher photosynthetic rates at low PPFD (Barreiro, 1992; Zhang et al., 2004; Tateno and Taneda, 2007). Our results showed that the photosynthetic capacity of the leaves (the maximum rate at which leaves can fix carbon during photosynthesis) was higher under W300 than under W700, which indicated that the photosynthetic capacity or potential was attenuated under a PPFD of 700 μmol m^{-2} s^{-1} (Figure 2.4). Long-term exposure of plants to excessive light leads to the production of large amounts of reactive oxygen species, thereby superseding the capacity of antioxidant systems and resulting in irreversible photooxidative damage to the chloroplast and cells, thus inhibiting photosynthesis (Karpinski et al., 1997; Karpinski et al., 1999). Hence, the PPFD of 700 μmol m^{-2} s^{-1} might have been too high for the efficient production of 'Micro-Tom'.

2.4.2. Experiment 2: light quality effect

Light quality can alter plant morphology by photoreceptors and signal transduction systems (Smith, 1982; Goto, 2003). Light quality affected the stem length and total dry weight in Experiment 2 (Table 2.7). In contrast to blue light, red light is known to increase the length of hypocotyl and plant height (Mazzella et al., 1997; Liu et al., 2011; Nanya et al., 2012). Our findings were consistent with this observation in Experiment 2, which showed that the stem length of seedlings grown under R9B1 light was the highest (Table 2.7). In contrast, the plants grown under R3B1, which had a higher percentage of blue light, produced significantly less dry mass than those grown under R9B1. This result was consistent with the finding that a high percentage of blue light can inhibit biomass production (Nishio, 2000; Snowden et al., 2016; Kong and Nemali, 2021).

Like PPFD, light quality had little effect on the proportion of intercepted light 6 DAT (Figure 2.5). However, the ratio of dry biomass produced during the period was 0.50:0.46:0.56 (≈1.0:0.9:1.1). McCree (1971) elucidated that the relative quantum efficiency of single leaves under blue light (400–500 nm) was 65–75% of that under red light (600–700 nm). In addition, a higher fraction of blue light led to lower Pn (Figure 2.6) and ϕ (Table 2.9), and this trend was similar to the changes in RUE (Table 2.8). This may explain the reason for the highest RUE of plants under the lowest fraction of blue light (R9B1). Therefore, R9B1 was the proper light quality for 'Micro-Tom' cultivation at the vegetative growth stage to increase the growth and RUE.

However, this does not necessarily mean that a greater proportion of red light leads to a higher RUE. In Experiment 2, R3B1 had a higher proportion of red light compared with W. In contrast, RUE was higher under W than under R3B1. McCree (1971) found that the relative quantum efficiency of green light (500–600 nm) was not inferior to that of blue light. In addition, green light can penetrate deeper into the canopy than red and blue light and improve the photosynthesis of single leaves and whole plants (Terashima et al., 2009; Nishio, 2000), which might be the reason for the higher RUE of plants under the highest fraction of green light (W) than under R3B1. Dong et al. (2014) reported a similar case in wheat plants and found that both net photosynthetic rate and stomatal conductance of leaves under monochromatic red light and a combination of red and blue lights were lower than those under white light.

Red light does not promote chlorophyll synthesis but sometimes inhibits it (Sood et al., 2005; Naznin et al., 2019; Chen et al., 2021). This was corroborated by our results of Experiment 2, in which chlorophyll concentration was the highest under the lowest red light fraction in W (Table 2.11). The highest chlorophyll concentration under W caused the lowest reflectance of leaves under green light (500–599 nm) among the three treatments (Table 2.10).

The effects of PPFD and light quality on dwarf tomatoes were different. Light quality had a significant effect on stem length, unlike PPFD. PPFD significantly affected LA, SLA, and leaf optical properties and changed the intercepted light proportion. Light quality did not significantly affect LA, SLA, light absorptance of leaves, or the intercepted light proportion. However, only one cultivar of dwarf tomato was used in this study, and the effects of PPFD and light quality on the growth and RUE may differ among tomato cultivars. Therefore, more tomato cultivars with efficient environment control strategies may be studied in the future to popularize efficient tomato production in PFALs. Moreover, 200–300 μmol m^{-2} s^{-1} PPFD and light quality with an RB ratio greater than three are used in a lettuce-production PFAL which is the most popular PFAL type (Pennisi et al., 2019; Pennisi et al., 2020). Therefore, it is easy to efficiently produce dwarf tomatoes using a lettuce-production PFAL after simple modification.

2.5. Conclusions

In this study, we evaluated the effects of PPFD and light quality on the growth and RUE in the dwarf tomato cultivar 'Micro-Tom'. The results demonstrated that higher PPFD caused higher dry mass production and lower SLA, but hardly affected the stem length. In addition, higher PPFD increased the Pn of individual leaves but decreased the RUE of the canopy. This was probably because the ϕ decreased with increasing PPFD. A PPFD of 700 μmol m^{-2} s^{-1} was excessive and decreased the photosynthetic capacity and chlorophyll concentration. Moreover, a high proportion of blue light inhibited dry mass production with the same intercepted light because leaves under a higher blue light proportion had lower Pn and ϕ. In conclusion, 300 μmol m^{-2} s^{-1} PPFD and R9B1 are recommended for 'Micro-Tom' cultivation at the vegetative growth stage to improve the RUE. The results of our study would be helpful in efficient tomato production in PFALs. Further study is necessary to determine a proper light condition for the reproductive growth stage to produce fruits by improving the RUE.

2.6. Supplementary materials

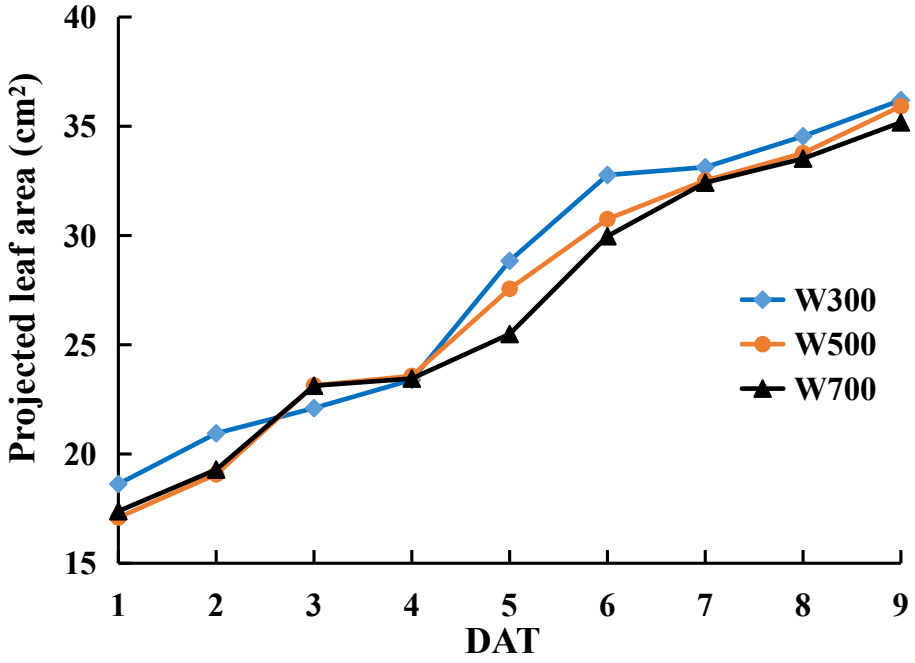

Figure S2.1 Effect of photosynthetic photon flux density (PPFD) on the projected leaf area (PLA) per plant of 'Micro-Tom' in Experiment 1. DAT represents days after treatment. Photographs of the canopy were taken from the top every day, and PLA per plant was determined from the photographs from 1 to 9 DAT. W300: 300 µmol m^{-2} s^{-1} PPFD, W500: 500 µmol m^{-2} s^{-1} PPFD, W700: 700 µmol m^{-2} s^{-1} PPFD.

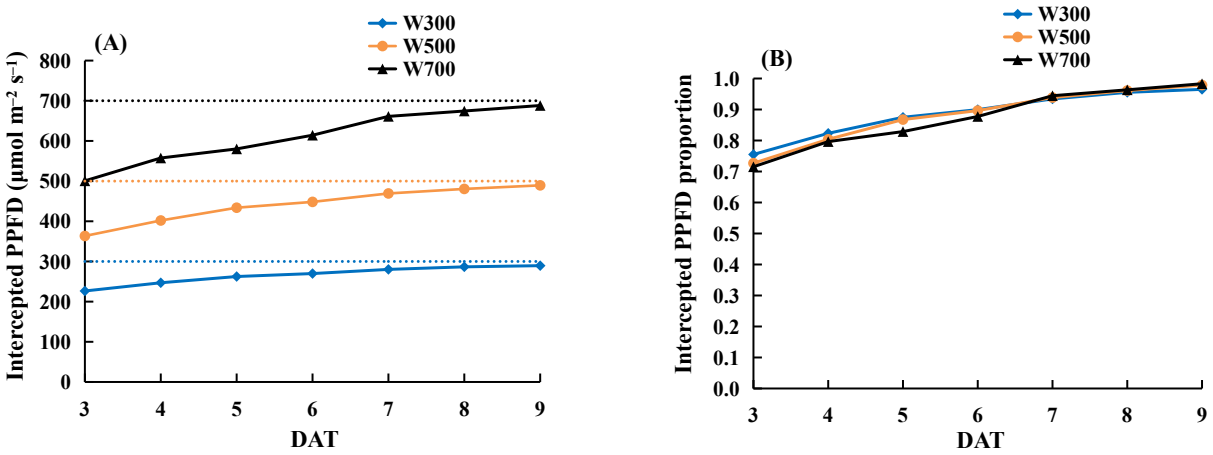

Figure S2.2 Effects of PPFD on the daily average of intercepted PPFD **(a)** and daily average of intercepted proportion **(b)** of the canopy in 'Micro-Tom' in Experiment 1. The intercepted PPFD of the canopy was calculated as the difference between the average PPFD on the top and bottom of the canopy. The intercepted PPFD proportion was calculated as the ratio of the intercepted PPFD to the average PPFD above the top of the canopy. DAT represents days after treatment. W300, W500, and W700 denote 300, 500, and 700 μmol m^{-2} s^{-1} PPFD, respectively.

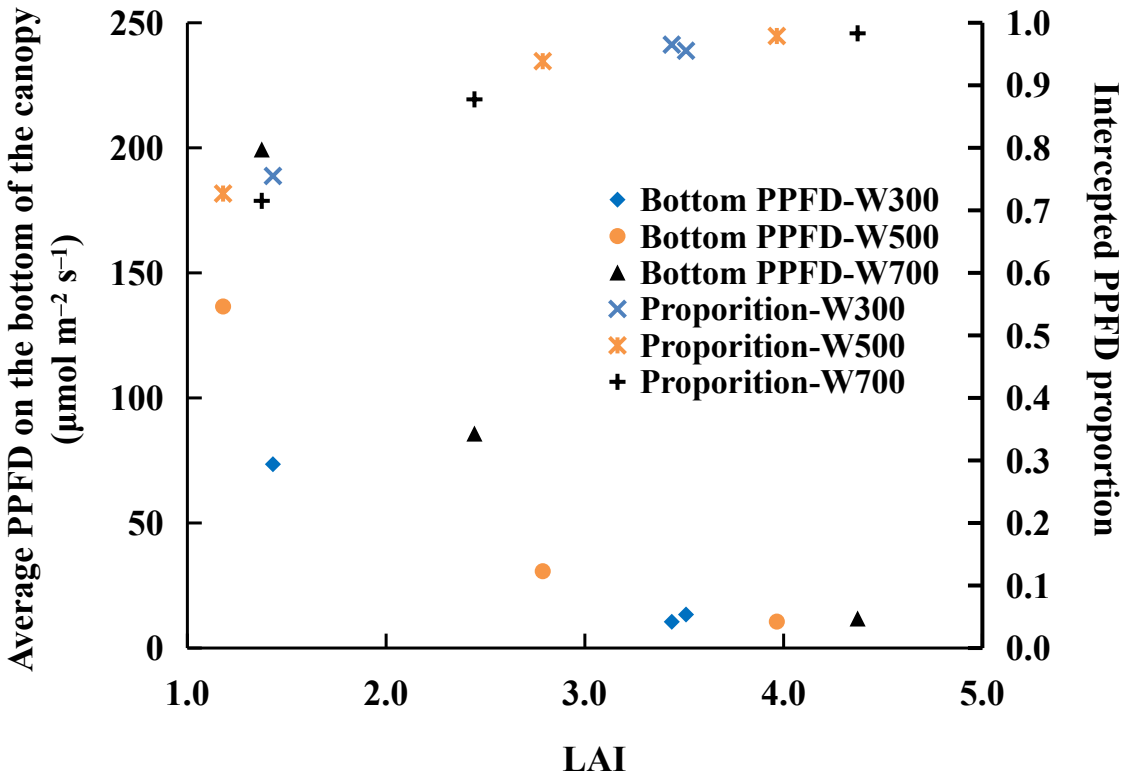

Figure S2.3 Relationships between leaf area index (LAI) and average PPFD on the bottom of the canopy and intercepted PPFD proportion under different PPFD in Experiment 1. LAI was defined as the ratio of leaf area to cultivation area. The intercepted PPFD proportion was calculated as the ratio of the intercepted PPFD to the average PPFD above the top of the canopy. W300: 300 μmol m^{-2} s^{-1} PPFD, W500: 500 μmol m^{-2} s^{-1} PPFD, W700: 700 μmol m^{-2} s^{-1} PPFD.

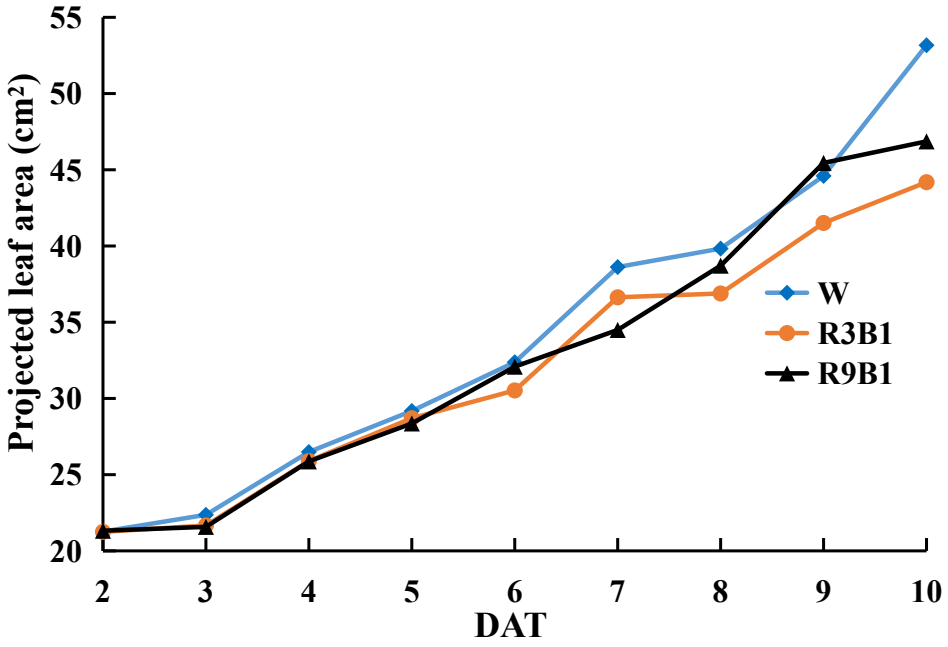

Figure S2.4 Effect of light quality on the PLA of 'Micro-Tom' in Experiment 2. DAT represents days after treatment. Photographs of the canopy were taken from the top every day and PLA per plant was determined from the photographs from 2 to 10 DAT. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

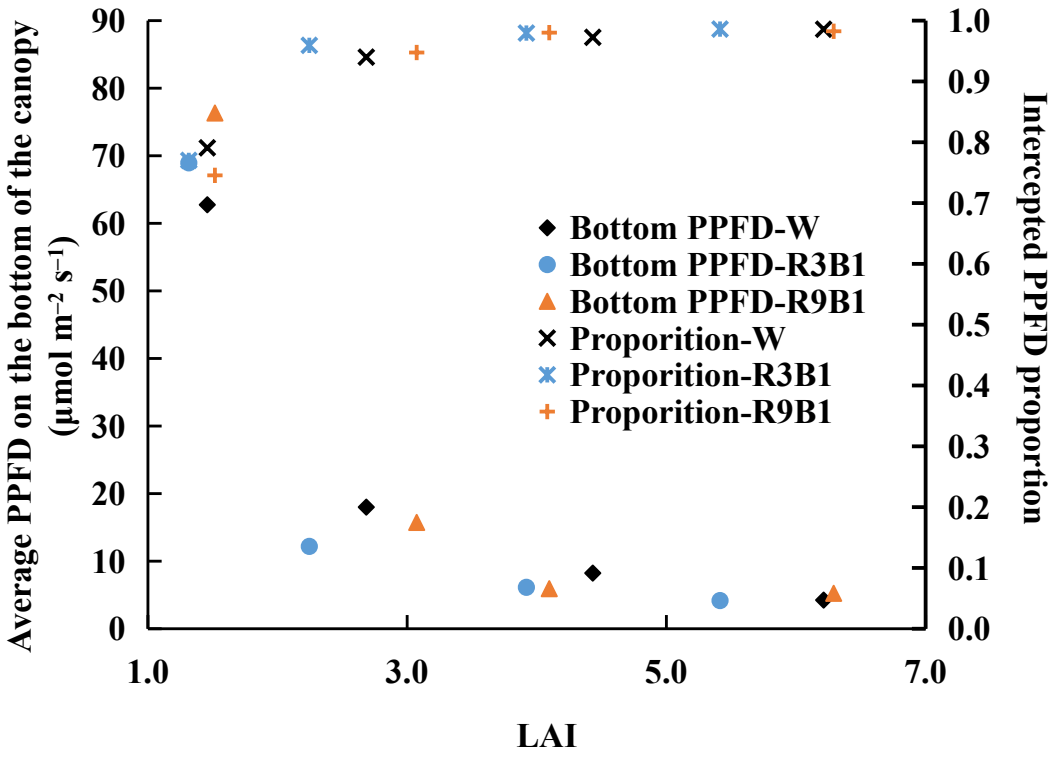

Figure S2.5 Relationships between LAI and average PPFD on the bottom of the canopy and intercepted PPFD proportion under different light qualities in Experiment 2. LAI was defined as the ratio of LA (cm^2) to cultivation area (cm^2). The intercepted PPFD proportion was calculated as the ratio of the intercepted PPFD to the average PPFD above the top of the canopy. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

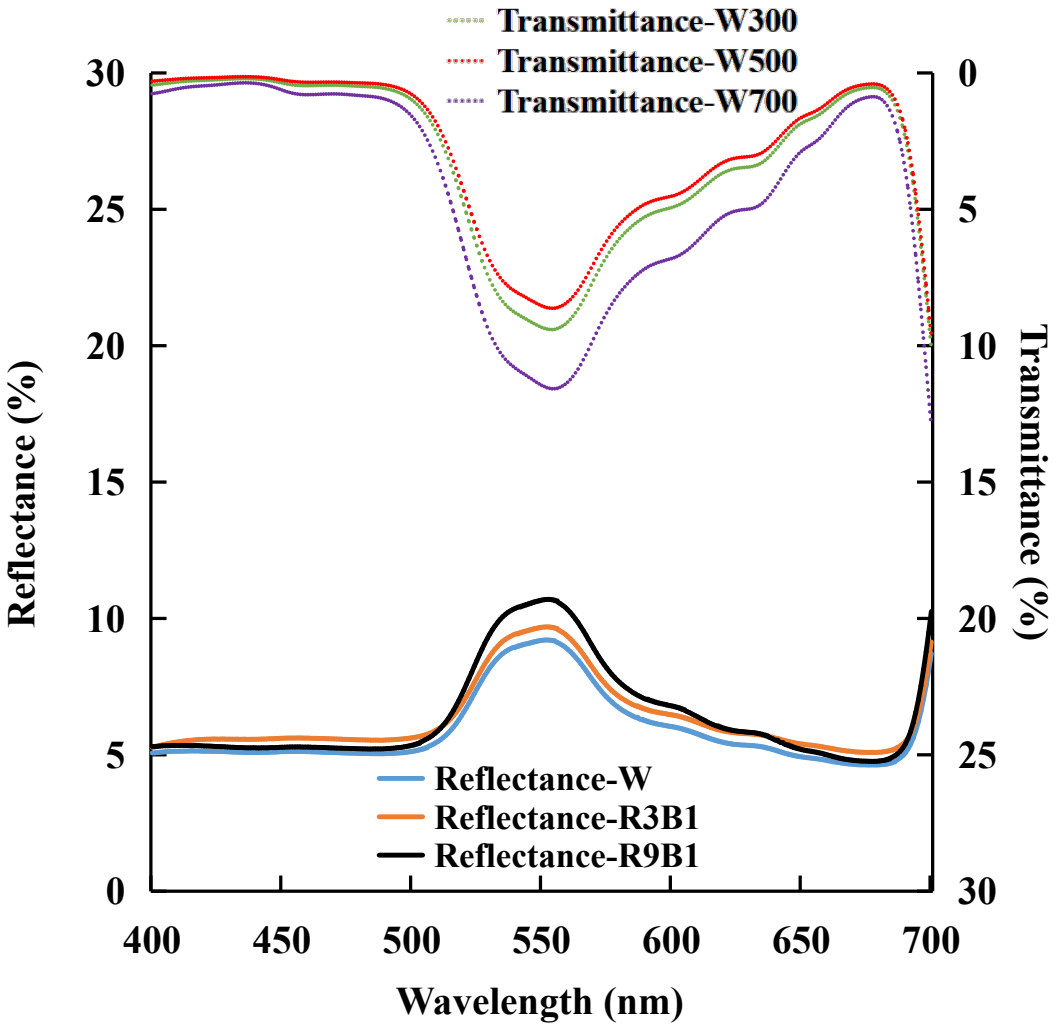

Figure S2.6 Effects of light quality on the reflectance and transmittance spectra of leaves in 'Micro-Tom' 10 DAT in Experiment 2. The range of the measured light spectrum was 400–700 nm. Each value represents the average of four plants. The PPFD of three treatments was set at 300 μmol m^{-2} s^{-1}. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

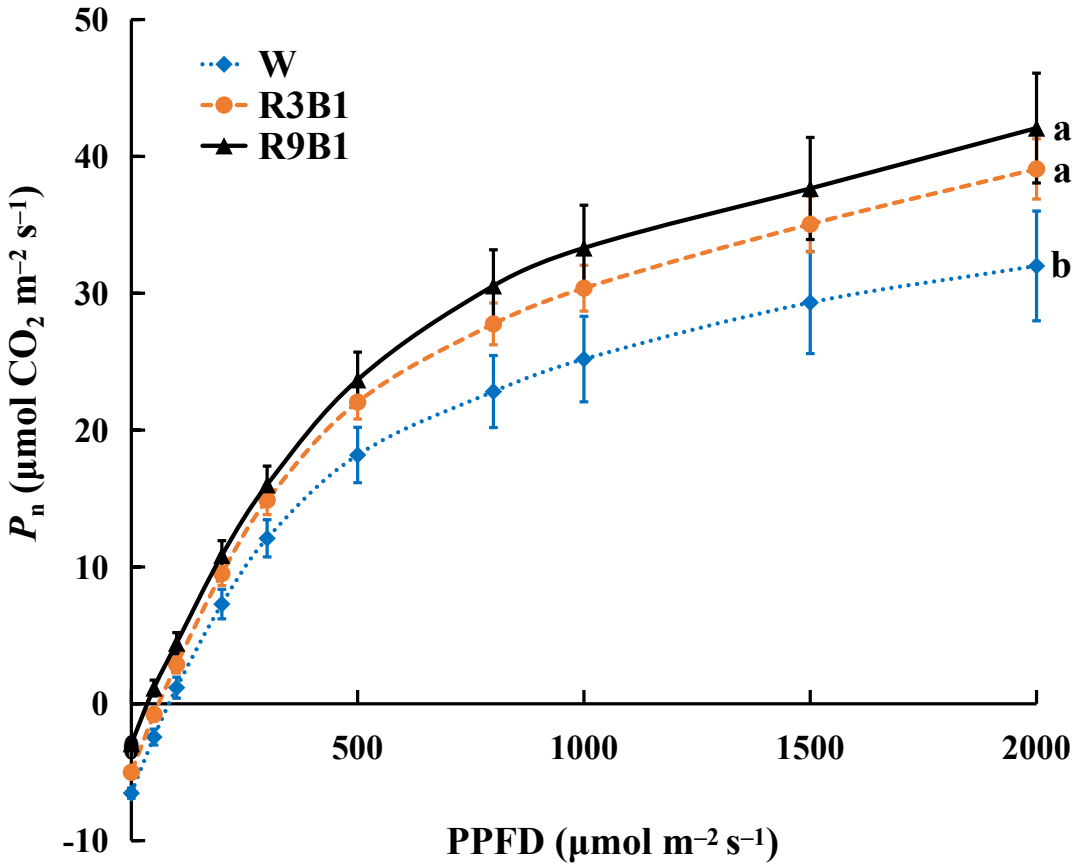

Figure S2.7 Light response curve of net leaf photosynthetic rate in 'Micro-Tom' 11 DAT in Experiment 2. Each value represents the average of three plants. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey-Kramer's test at $p < 0.05$. W: white light; R3B1: red/blue ratio = 3; R9B1: red/blue ratio = 9.

Figure S2.8 'Micro-Tom' seedlings grown under different PPFDs 10 DAT in Experiment 1. W300: 300 μmol m^{-2} s^{-1} PPFD, W500: 500 μmol m^{-2} s^{-1} PPFD, W700: 700 μmol m^{-2} s^{-1} PPFD.

CHAPTER 3.

Effect of PPFD on FBRUE of dwarf tomatoes under LED light at the reproductive growth stage

3.1. Introduction

Small-sized and short-season (Sun et al., 2006) dwarf tomatoes have the potential to become commercial fruit vegetables cultivated in a plant factory with artificial light (PFAL), otherwise known as vertical farm. They also have other advantages, such as low light requirement (Kato et al., 2011) and high planting density (Meissner et al., 1997), compared to general tomato varieties. However, fruit vegetables such as tomatoes have longer growth cycles and lower harvest indices than leafy vegetables such as lettuce. A lower harvest index indicates that more dry mass production is required for the same yield. Therefore, more energy and electricity are required in a PFAL to produce tomatoes with the same yield as leafy vegetables.

More than half of the electric power is used for lighting in a PFAL (Ohyama et al., 2002; Graamans et al., 2018). Therefore, a significant reduction in electricity cost can be achieved by improving the light-use efficiency. Radiation-use efficiency (RUE) can be defined as the ratio of the dry biomass produced to the amount of photosynthetically active radiation (PAR) captured by the crop and is a classic and important parameter for measuring radiation utilization in crops (Williams et al., 1965; Shibles and Weber, 1966). Tomato plants are divided into two main parts: edible (fruits) and inedible (roots, stems, and leaves) parts. Fruit biomass radiation-use efficiency (FBRUE) can be defined as the ratio of the dry mass of a plant's fruits to the number of photosynthetic photons captured by the plant. It is an important index for the commercial production of tomatoes, indicating the distribution of photoassimilates in fruits. Additionally, FBRUE is a bridge linking photosynthesis and production output.

For general cultivars, the FBRUE of tomato was 0.3 g mol^{-1} in NASA's Biomass Production Chamber (Wheeler et al., 2008), 0.2 g mol^{-1} in a closed plant production system (Goto, 2011), and 0.36 g mol^{-1} in the Permanent Astrobase Life-support Artificial Closed Ecosystem (Li et al., 2019) when tomatoes were harvested. Therefore, there is still room for improvement in FBRUE. However, few studies have been conducted to improve the FBRUE of dwarf tomatoes in PFALs.

Photosynthetic photon flux density (PPFD) is an important environmental factor

affecting RUE and dry matter distribution, further affecting FBRUE. At the vegetative growth stage, a higher PPFD led to lower RUE in a dwarf tomato cultivar 'Micro-Tom' from 300 to 700 μmol m^{-2} s^{-1} PPFD (Ke et al., 2021). In addition, PPFD influences the dry mass distribution to fruits. Yan et al. (2018) reported that the dry matter partitioning of tomato (cultivar, 'Ruifen882') fruits under supplementary artificial light (total daily PAR integral of 15.4 mol m^{-2}) was higher than that without supplementary light (total daily PAR integral of 12.4 mol m^{-2}). However, the effects of PPFD on biomass production and its distribution to plant organs are highly cultivar- and growth-stage-specific. Compared to cultivars with large fruits, Dueck et al. (2010) found that supplementary lighting had less effect on cherry tomatoes in commercial crop management. Plant biomass production and yield are related to the source strength and fruit sink strength, respectively (Heuvelink, 1996; Marcelis, 1996). However, no study has elucidated the effects of PPFD on the source and fruit sink strengths of dwarf tomatoes in PFALs.

This study had two main objectives. One was to analyze the effect of PPFD on the FBRUE of dwarf tomatoes and to determine a suitable PPFD for enhancing FBRUE at the reproductive growth stage. The other was to identify the effects of PPFD on the source strength and fruit sink strength of dwarf tomatoes during the reproductive growth stage.

3.2. Materials and methods

3.2.1. Plant material and growth condition

We used a dwarf tomato cultivar, 'Micro-Tom' (*Lycopersicon esculentum*), as the test material. Tomato seeds were sown in urethane sponges and kept under dark conditions for three days at 25 °C. The plants were cultivated under white LED lamps (LDL40S-N19/21, Panasonic Corporation, Osaka, Japan) after germination at a PPFD of 200 μmol m^{-2} s^{-1} in a cultivation room at the Matsudo campus, Chiba University, Japan. The environmental elements of the cultivation rooms are listed in Table 3.1. A 1/2 OAT house A nutrient (OAT Agrio Co., Ltd., Tokyo, Japan) was used 10 days after germination for all plants. The electrical conductivity (EC) and pH of the nutrient solution were set at 1.3 dS m^{-1} and 6.3, respectively. The nutrient solution was renewed weekly.

Table 3.1 Environmental elements in the cultivation room.

Environmental elements	Set value
Photoperiod (h d^{-1})	16
Air temperature (light/dark) (°C)	25/20
Relative humidity (%)	65–70
CO_2 concentration (μmol mol^{-1})	1000

According to our previous study (Ke et al., 2021), red and blue LED lamps (CIVILIGHT, DPT2RB120Q33 40 type, Showa Denko K.K., Tokyo, Japan; R:B = 9:1) were used for cultivation 24 days after sowing (DAS). In addition, the PPFD at the canopy top was set to 300 μmol m^{-2} s^{-1}. As uniform seedlings bloomed, they were evenly transferred and placed on four polystyrene foam boards in four containers (18.6 L, L 600 mm × W 300 mm × H 141 mm, SANKO Co. Ltd., Tokyo, Japan) at 35 DAS. Each container was subjected to one of the four treatments with different PPFDs in a growth chamber equipped with white LED lamps (customized lamp, color temperature: 4000 K; Showa Denko K. K., Tokyo, Japan). The different light treatments were: W200 (PPFD: 200 μmol m^{-2} s^{-1}, daily light integral (DLI): 11.52 mol m^{-2} d^{-1}), W300 (PPFD:

300 μmol m^{-2} s^{-1}, DLI: 17.28 mol m^{-2} d^{-1}), W500 (PPFD: 500 μmol m^{-2} s^{-1}, DLI: 28.80 mol m^{-2} d^{-1}), and W700 (PPFD: 700 μmol m^{-2} s^{-1}, DLI: 40.32 mol m^{-2} d^{-1}). A spectroradiometer (USR-45DA; USHIO Inc., Tokyo, Japan) was used to measure the spectral photon flux distributions of the LED lamps (Figure 3.1). The environmental elements, except for the light condition, were the same as before transplanting. pH and EC of the nutrient solution were set at 6.0 and 2.1 dS m^{-1}, respectively. The seedlings were planted at a density of 238.1 plant m^{-2}. Axillary buds and side shoots were pruned after appearance.

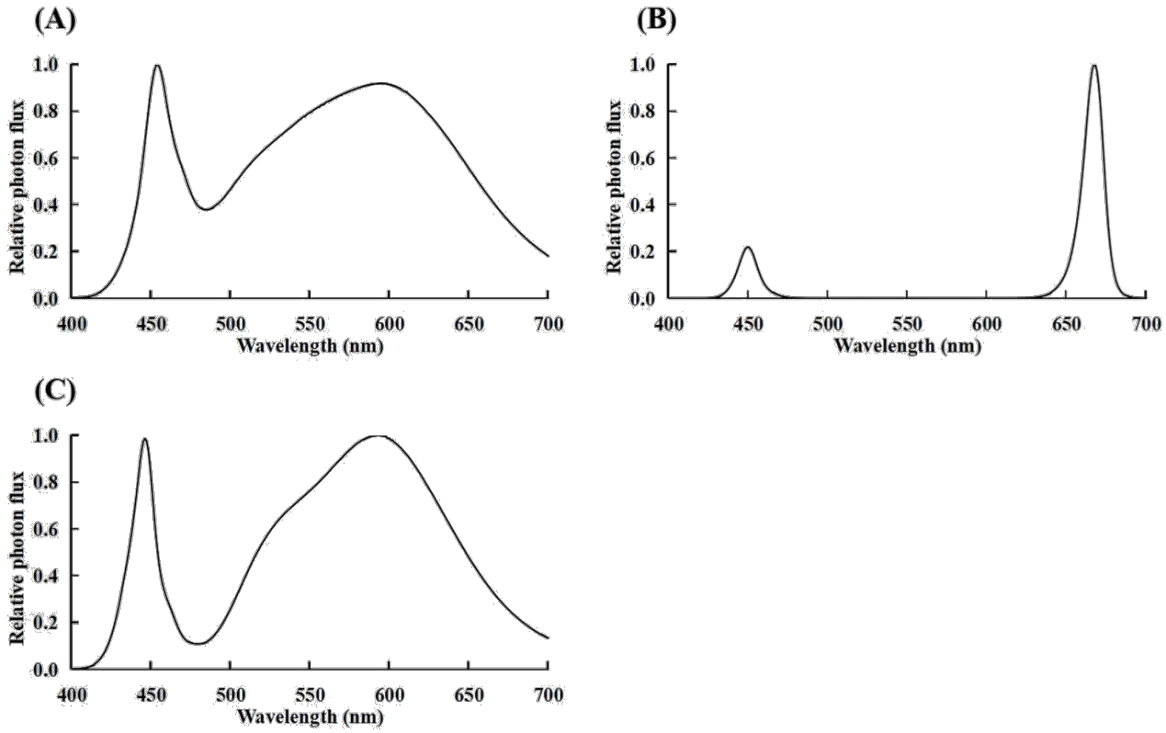

Figure 3.1 Spectral photon flux distributions of (A) white lamps (LDL40S-N19/21) until 24 days after sowing (DAS), (B) red and blue (red:blue = 9:1) LED lamps (CIVILIGHT) from 24–35 DAS, and (C) white LED lamps (customized lamp) after 35 DAS. The maximum value of photon flux was converted to 1.0.

At 36 DAS, plants in each light treatment (except W200) were separated into three groups: not pruned (NP; 44 plants), pruned to one fruit per plant (OFP; 16 plants), or one fruit per truss (OFT; 4 plants). 'Micro-Tom' is a determinate tomato with no new leaf on the main stem after the first truss. Therefore, plants with one fruit per truss were

used to test whether the fruit growth in the OFP reflected potential growth. If there was no significant difference in fruit size/dry weight when fruit load was doubled or tripled (OFP fruits vs. OFT fruits), then the fruit size/dry weight of OFP plants can be regarded as potential fruit growth. All plants, except those that did not receive fruit pruning, had their proximal fruits removed during anthesis.

3.2.2. Growth measurement

Three or four NP plants in each treatment were destructively sampled for biomass and leaf area measurements at 36, 43, 50, 57, 64, 71, and 82 DAS. Fresh and dry weights of the plant organs (leaves, stems, fruits, and roots) were measured. Plant height was measured from the base of the main stem to the top using a ruler. The leaf area (LA, cm^2) was measured using a leaf area meter (LI-3000C, Li-Cor Inc., Lincoln, NE, USA). Specific leaf area SLA ($cm^2\ g^{-1}$) was determined by dividing LA (cm^2) by leaf dry weight (g). The number of fruits and anthesis dates for each fruit were recorded.

3.2.3. Fruit quality

Brix and acidity of 7–8 ripe tomatoes from four NP plants in every treatment were measured with a pocket Brix-Acidity Meter (PAL-BX|ACID3; Atago Co. Ltd.) as parameters of fruit quality at 82 DAS.

3.2.4. Leaf optical properties

A spectrophotometer (V-750, JASCO Corporation, Tokyo, Japan) was used to measure the reflection and transmission spectra of the first leaf from the top of the main stem (fully expanded and unshaded leaf) at 82 DAS of the plant with an integrating sphere unit (ISV-922, JASCO Corporation, Tokyo, Japan). The measured light spectrum ranged from 400 nm to 700 nm. Three or four NP plants were sampled per treatment. For each wavelength, the absorptance was calculated as 100% minus reflectance and transmittance.

3.2.5. Light response curve, photosynthetic quantum yield (ϕ), and photosynthetic capacity (P_{max}) of leaves

The response of net photosynthetic rate (Pn) to PPFD was also determined on the first leaf from the top of the main stem using a portable photosynthesis measurement system (LI-6400XT, LI-COR Inc., Lincoln, NE, USA), equipped with a 6400-02B LED light source (90% red light with a peak at 665 nm and 10% blue light with a peak at 470 nm) in a leaf chamber at 36, 64, and 82 DAS. Initially, the leaves were clamped into a cuvette at 1000 μmol m^{-2} s^{-1} PPFD until stomatal conductance, and Pn remained stable. A PPFD gradient of 2000, 1500, 1000, 800, 500, 300, 200, 100, 50, and 0 μmol m^{-2} s^{-1} was applied to the leaf surface. A leaf temperature of 25 ± 1 ˚C, relative humidity of 65–70%, and 1000 μmol mol^{-1} CO_2 concentration were set. A flow rate was set at 500 mol s^{-1} to allow air to flow through the system. Three NP plants were measured for each treatment group. The photosynthetic quantum yield (ϕ, mmol CO_2/mol photon) is the ratio of the net photosynthetic rate to PPFD on the leaf (Singsaas et al., 2001; Skillman, 2008). As a result of fitting light response curves to a non-rectangular hyperbolic function (Cannell and Thornley, 1998), the photosynthetic capacity was derived (maximum net photosynthetic rate, P_{max}).

3.2.6. RUE

Radiation-use efficiency (RUE) (g mol^{-1}) was defined as the ratio of the accumulated total dry weight (W, g) to the integrated PPFD (I_{PPFD}, mol) received by a plant.

The I_{PPFD} (mol) until day t_1 is calculated as follows:

$$I_{PPFD}=T\times\sum_{t=0}^{t_1}[PLA(t)\times(PPFD_T-PPFD(t))] \quad (0<t\leq t_1) \tag{3-1}$$

where T is the light period of one day, 5.76×10^4 s (16 h×3600 s h^{-1}), $PLA(t)$ is the projected leaf area (m^2) of the plant on day t, $PPFD_T$ (mol m^{-2} s^{-1}) is the PPFD at the top of the canopy and was set as a specific constant for each treatment, and $PPFD(t)$

(mol m^{-2} s^{-1}) is the PPFD at the bottom of the canopy on day *t*.

To maintain PPFDs at the top of the canopies, a quantum sensor (LI-190, Lincoln, NE, USA) and GaAsp photodiodes (G1118, Hamamatsu Photonics K. K., Shizuoka, Japan) were used, and the PPFDs were maintained at 200, 300, 500, and 700 μmol m^{-2} s^{-1} in W200, W300, W500, and W700, respectively. Quantum sensors and GaAsp photodiodes were used to measure the PPFD of 29–51 evenly distributed points at 36, 37, 38, 40, 42, 45, 47, 49, 55, 58, 63, 65, 69, 72, 75, 78, and 81 DAS at the bottom of the canopy. The intercepted PPFD of the canopy was equal to the difference between the average PPFD at the top and bottom. The intercepted PPFD proportion was calculated by dividing the intercepted PPFD by the average PPFD at the canopy top. The intercepted PPFD proportion and PLA between two consecutive measured values increased linearly, and those on unmeasured days were estimated based on the measured values.

Free imaging software (LIA 32 ver. 0.378, Yamamoto) was used to determine the projected leaf area (PLA) from photos of the canopy on the same days that PPFD measurements were taken.

The RUE and integrated PPFD received by the plant until 36 DAS were estimated as 1.36 g mol^{-1} and 0.6 mol, respectively, based on the data shown in our previous study (Ke et al., 2021), respectively. The PLA of the canopy, rather than the individual plant, was determined for each measurement. The fitted regression line slope to illustrate the relationship between W and I_{PPFD} was used to evaluate RUE during the entire reproductive growth stage.

3.2.7. Fruit biomass radiation-use efficiency (FBRUE)

It is possible to analyze the effects of PPFD on the FBRUE of a plant by breaking the effect down into its individual components (Figure 3.2). In this analysis, FBRUE is the product of RUE (g mol^{-1}), and the fraction of dry mass partitioned into fruits (F_{fruits}, g g^{-1}) on a given day, as shown in the following formula:

$$FBRUE = RUE \times F_{fruits} \quad (3\text{-}2)$$

F_{fruits} (g g^{-1}) is defined as the ratio of the dry mass of tomato fruits to the total dry mass of the plant and is calculated using the following formula:

$$F_{fruits}=\frac{W_{fruits}}{W} \tag{3-3}$$

where W_{fruits} (g) is the fruit dry weight, and W (g) is the dry weight of the whole plant on a given day.

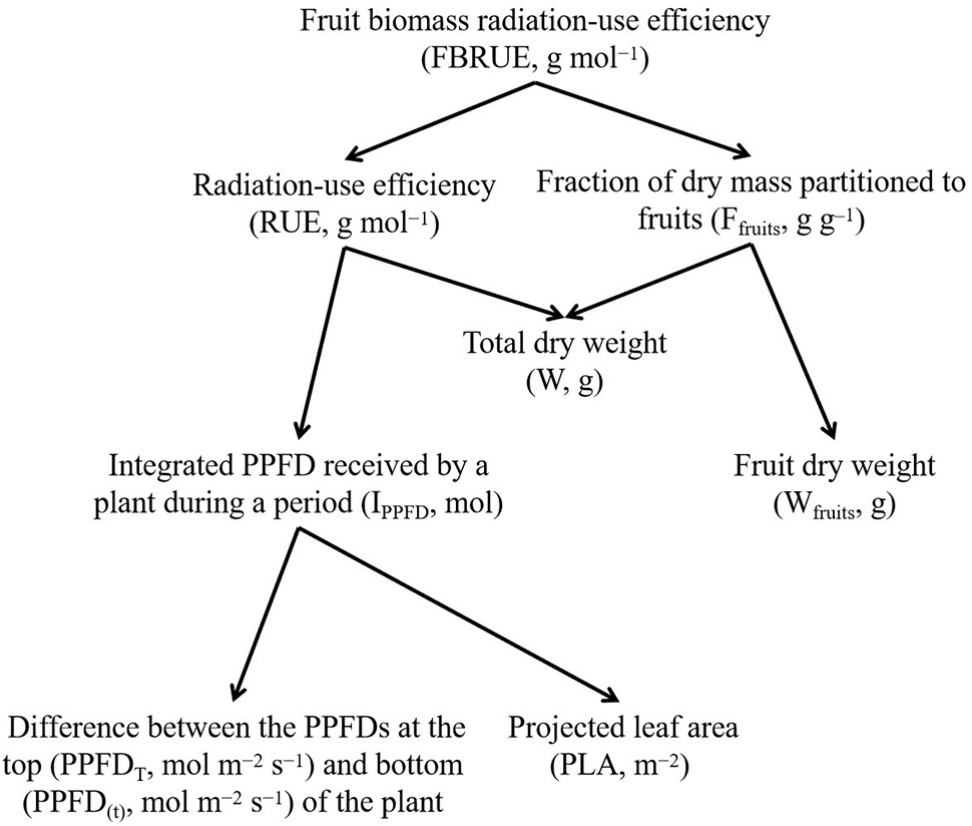

Figure 3.2. The scheme of fruit biomass radiation-use efficiency (FBRUE) was segregated into underlying components. Arrows indicate the calculation of the parameters (i.e., lower-level components are required to calculate the parent parameters). Abbreviations and units for each component are indicated in parentheses.

3.2.8. Source strength and fruit sink strength

Cumulative dry mass production of a 'Micro-Tom' plant from 36 to 84 DAS follows an exponential function in time according to a preliminary experiment and the present experiment (measured values shown in Figure S3.1 and the goodness of fit in

present experiment shown in Table S2.1). Therefore, the total dry weight of a plant over time was calculated as follows:

$$W(t)=\alpha \cdot e^{\beta t} \quad (3\text{-}4)$$

where $W(t)$ (g) is the total dry weight of the plant on t DAS, α and β are the coefficients based on the fitting function for the measured values.

The absolute growth rate is used as an estimate of the source strength (S_{source}), which can be calculated as

$$S_{source}(t)=\frac{dW(t)}{dt} \quad (3\text{-}5)$$

where $S_{source}(t)$ (g d^{-1}) is the rate of increase in total dry weight per plant on t DAS.

Fruit sink strength ($S_{fruit\text{-}sink}$) is the sum of the sink strength of each fruit in a plant.

3.2.9. Sink strength of a single fruit

The sink strength of a single fruit can be quantified by calculating its potential growth rate (i.e., growth under non-limiting assimilate supply conditions). In this study, a non-destructive measurement of the hypothetical growth potential of fruits (i.e., one fruit per plant) was performed based on the method of Li et al. (2015).

The observation of fruit volume and age of plants with one fruit per plant was used to estimate the potential growth rate of a single fruit. The shape of the tomatoes was assumed to be an elliptical sphere. Therefore, the volume of a tomato fruit was calculated as follows: fruit length × width × height × π/6. Measurements of the four OPF and four OPT plants were performed every three days.

The results demonstrated that the relationship between fruit volume and fresh weight of non-pruned fruits was almost the same as that of potential-growth fruits in 'Micro-Tom' (Figure S3.2). To establish a linear regression between fruit volume and fresh weight, randomly selected fruits were collected from the NP plants in each light treatment.

Wubs et al. (2012) used a 4th-degree (or 3rd-degree) polynomial function to express the relationship between fruit age and dry matter content of individual fruits ($IDMC_{fruit}(x)$).

$$IDMC_{fruit}(x)=ax^4+bx^3+cx^2+dx+e \quad (3\text{-}6)$$

where *a, b, c, d,* and *e* are the coefficients and *x* is the fruit age (days after anthesis, DAA). Preliminary experiments showed that pruning did not affect the relationship between fruit age and dry matter content in 'Micro-Tom' plants (data not shown). The dry weight of an individual fruit ($IW_{fruit}(x)$) can be the product of $IDMC_{fruit}(x)$ and fresh fruit weight at *x* DAA.

Moreover, the Gompertz function can be used to fit the dry weight of individual fruits based on their age (Ji et al., 2020):

$$IW_{fruit}(x)=IW_{max}\cdot e^{-k(x-x_m)} \quad (3\text{-}7)$$

where IW_{max} is the maximum dry weight of the fruit (g), k is the growth rate coefficient, and x_m is the fruit age (DAA) at the maximum growth rate.

Based on the derivative of the Gompertz function, we obtained the growth rate of individual fruit (IGR_{fruit}, g d^{-1}) in relation to fruit age:

$$IGR_{fruit}(x)=IW_{fruit}(x)\cdot k\cdot e^{-k(x-x_m)} \quad (3\text{-}8)$$

Each fruit growth curve was fitted using a nonlinear mixed model, which assumed that measurements made on one fruit were grouped while assuming that the variation between measurements made on one fruit was lower than those made on different fruits.

3.2.10. The power of lamps

Power consumption of LED lamps in each treatment was measured by a portable power monitor (Omron ZN-CTX21, OMRON Corporation, Kyoto, Japan).

3.2.11. Statistical analysis

One-way analysis of variance (ANOVA) was performed using SPSS for Windows (Version 24.0; SPSS Inc., Chicago, IL, USA) to analyze the data. A Tukey-Kramer test at $p < 0.05$ was used to compare the mean values of measured data to investigate significant differences among treatments.

3.3. Results

3.3.1. Growth characteristics

PPFD significantly affected the specific leaf area (SLA), total fresh and dry weights, and total dry matter ratio (Table 3.2). SLA decreased with an increase in PPFD and was the lowest in W700. There were no significant differences in the total fresh and dry weights between W200 and W300. Total fresh and dry weights as well as total dry matter ratio increased with an increase in PPFD from 300 to μmol m^{-2} s^{-1}. They were significantly higher under 700 μmol m^{-2} s^{-1} of PPFD than under 200 and 300 μmol m^{-2} s^{-1}. However, PPFD had no significant effect on the plant height.

Table 3.2 Effect of photosynthetic photon flux density (PPFD) on the growth of 'Micro-Tom' 82 days after sowing (DAS). Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ ($n = 3$−4). W200, W300, W500, and W700 denote 200, 300, 500, and 700 μmol m^{-2} s^{-1} PPFD treatments, respectively. All sampled plants are plants without pruning (NP plants).

Treatment	Plant height (cm)	Specific leaf area (cm^2 g^{-1})	Total fresh weight (g)	Total dry weight (g)	Total dry matter ratio (%)
36 DAS	9.9 ± 0.49	312.56 ± 17.88	10.00 ± 1.03	0.83 ± 0.09	8.40 ± 0.38
W200	13.1 ± 0.2	164.91 ± 4.97 a	109.69 ± 6.53 c	10.97 ± 0.46 b	9.60 ± 0.30 c
W300	11.3 ± 0.3	115.73 ± 4.83 a	104.56 ± 17.4 c	10.90 ± 1.78 b	10.45 ± 0.65 b
W500	10.7 ± 0.6	82.96 ± 3.67 b	125.15 ± 9.91 b	13.41 ± 1.10 ab	10.70 ± 0.71 b
W700	11.4 ± 0.9	66.66 ± 5.35 c	156.69 ± 8.30 a	18.00 ± 0.89 a	11.50 ± 0.17 a

3.3.2. Leaf optical properties

Photosynthetically active radiation (PAR) was significantly more reflected by the top leaves in W500 and W700 than by those in W200 and W300 (Table 3.3 and Figure S3.3). Additionally, the reflectance of leaves under green (500–599 nm) and red (600–700 nm) light increased with an increase in PPFD, and were significantly higher in

W500 and W700 than in W200 and W300 (Table 3.3). The absorptance under red light decreased with an increase in PPFD, and was significantly higher in W200 and W300 than in W500 and W700. The effects of PPFD on the optical characteristics of the leaves under green and red light were greater than those under blue light (400–499 nm) (Figure S3.3).

Table 3.3 Effects of PPFD on the reflectance and absorptance of leaves in 'Micro-Tom' at the green and red wavelengths 82 DAS. The range of measured light spectrum was 400–700 nm. Each value represents the mean ± standard error. Different letters in a column indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ ($n = 4$). All sampled plants are NP plants.

Treatment	Reflectance (%)		Absorptance (%)
	500–599 nm (Green)	600–700 nm (Red)	600–700 nm (Red)
W200	6.1 ± 0.7 c	5.2 ± 0.6 b	93.6 ± 0.4 a
W300	7.4 ± 0.5 b	5.8 ± 0.4 b	93.2 ± 0.5 a
W500	8.8 ± 0.9 a	7.2 ± 0.9 a	91.4 ± 1.2 b
W700	8.5 ± 1.1 a	7.1 ± 1.1 a	91.9 ± 1.2 b

3.3.3. Light response curve, ϕ, and P_{max} of leaves

The net leaf photosynthetic rate (Pn) of the first leaf increased rapidly and then slowly in all treatments at 43, 64, and 82 DAS (Figure 3.3A, B, and C). There were no significant differences in Pn measured at PPFDs from 0 to 2000 μmol m^{-2} s^{-1} among all treatments at 43 DAS (Figure 3.3A). However, the Pn of leaves grown under higher PPFD was lower than that of leaves grown under lower PPFD at the same measured PPFD at 64 and 82 DAS (Figure 3.3B and C). At 64 DAS, the Pn measured at PPFDs ranging from 0 to 800 μmol m^{-2} s^{-1} in W200 and W300 was significantly ($p < 0.05$) higher than that in W700 (Figure 3B). At 82 DAS, the Pn measured at PPFDs ranging from 50 to 2000 μmol m^{-2} s^{-1} in W200 was significantly ($p < 0.05$) higher than that in W700 (Figure 3.3C).

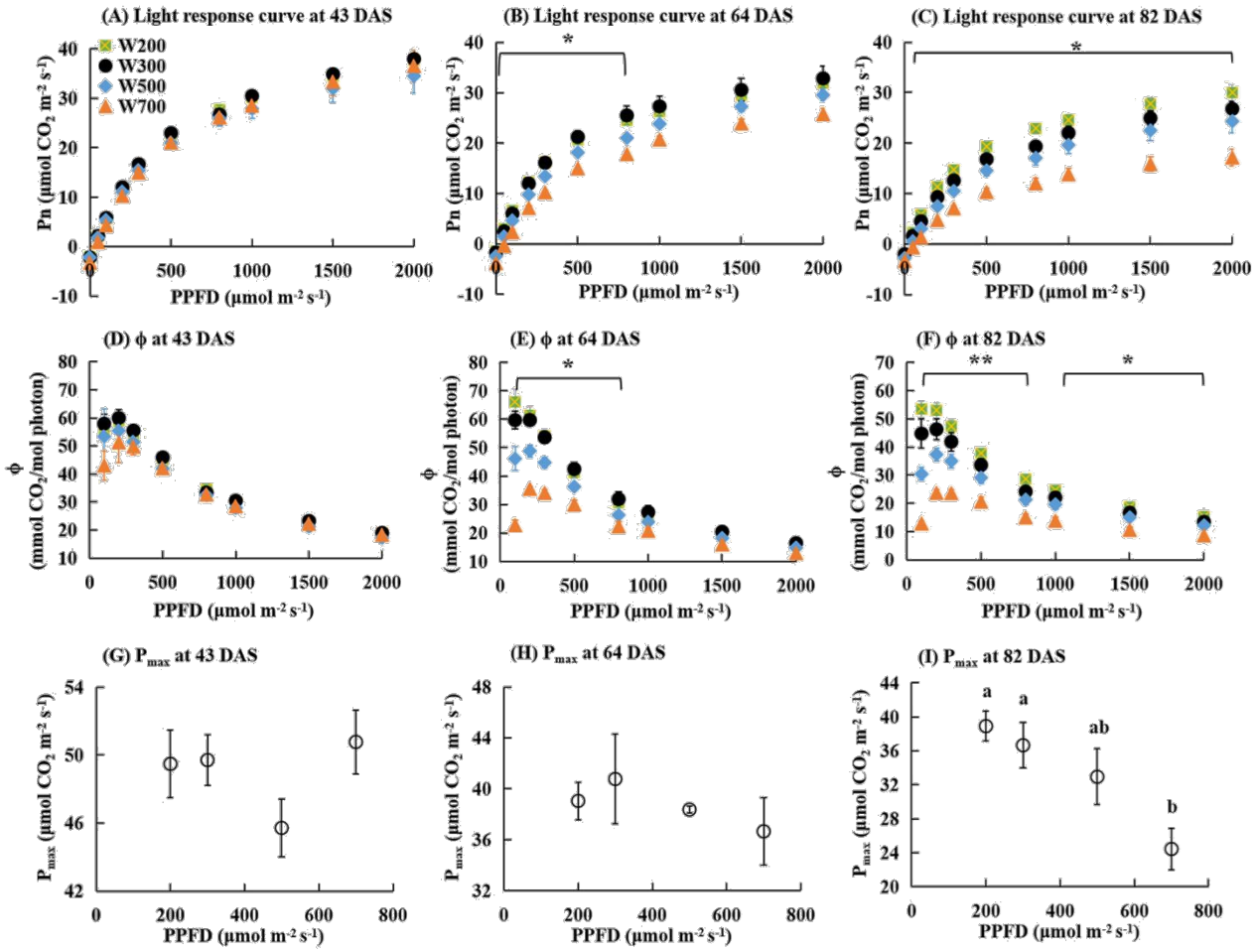

Figure 3.3 Effects of PPFD on light response curves of net leaf photosynthetic rate (Pn) 43 (A), 64 (B), and 82 (C) DAS, photosynthetic quantum yield (ϕ) 43 (D), 64 (E), and 82 (F) DAS, and photosynthetic capacity (maximum net photosynthetic rate, P_{max}) 43 (G), 64 (H), and 82 (I) DAS in 'Micro-Tom'. Error bars show ± standard error. The asterisks in (B), (C), (E) and (F) indicate significant differences among treatments based on Tukey−Kramer's test at $*p < 0.05$ and $**p < 0.01$ ($n = 3-4$). Different letters in (I) indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$. All sampled plants are NP plants.

The photosynthetic quantum yield (ϕ) in all treatments at 43 DAS (Figure 3.3D), in W300, W500, and W700 at 64 DAS (Figure 3E), and 82 DAS (Figure 3.3F) increased as PPFD increased from 100 to 200 μmol m^{-2} s^{-1} and then decreased as PPFD increased to 2000 μmol m^{-2} s^{-1}. There was no significant difference in the ϕ among all treatments at each PPFD at 43 DAS (Figure 3.3D). However, a higher PPFD led to a lower ϕ in

W200 at 64 DAS (Figure 3.3E) and 82 DAS (Figure 3.3F). At 64 DAS, the values ϕ in W200 and W300 were significantly higher than those in W700 at PPFDs ranging from 100 to 800 μmol m^{-2} s^{-1} (Figure 3.3E). In addition, the ϕ in W200 was significantly higher than that in W700 at PPFDs from 100 to 2000 μmol m^{-2} s^{-1} at 82 DAS (Figure 3.3F).

The maximum net photosynthetic rate (P_{max}) of the first leaf was not significantly different among treatments at 43 DAS (Figure 3.3G) and 64 DAS (Figure 3.3H). P_{max} decreased with increasing PPFD at 82 DAS (Figure 3.3I). The P_{max} under 700 μmol m^{-2} s^{-1} PPFD was significantly lower than that under 200 and 300 μmol m^{-2} s^{-1} PPFD. However, there were no significant differences in Pn, ϕ, or P_{max} between W200 and W300.

3.3.4. RUE

The fitted line slope in Figure 3.4 indicates RUE during the reproductive growth stage. RUE increased marginally when PPFD increased from 200 to 300 μmol m^{-2} s^{-1} and then decreased with an increase in PPFD from 300 to 700 μmol m^{-2} s^{-1}. The RUE was the highest (1.04 g mol^{-1}) in W300 and the lowest (0.78 g mol^{-1}) in W700 among the four treatments. The R^2 values for all the treatments were above 0.9.

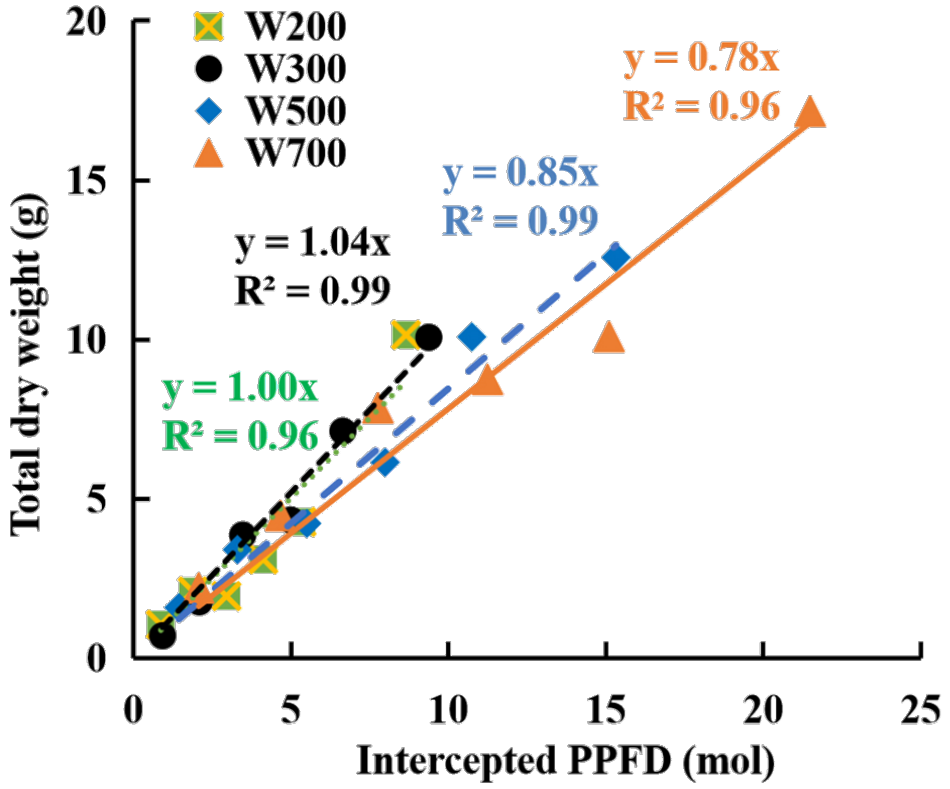

Figure 3.4 Relationships between accumulated total dry weights and cumulative intercepted PPFDs per plant in 'Micro-Tom' under different PPFDs during the reproductive growth stage. Each value represents the average of three or four NP plants. The slope of the fitted linear relationship is the radiation-use efficiency (RUE, g mol^{-1}) at the reproductive growth stage.

3.3.5. FBRUE component analysis

Fruit biomass radiation-use efficiency (FBRUE) component analyses under different PPFDs are shown in Figure 3.5 based on Figure 3.2 to quantity the effects of PPFD on increment or decrement of main factors of FBRUE. Percentages near the parameters in W300, W500, and W700 are the percentage increments relative to W200, as shown in Figure 3.5. FBRUE, RUE, and the fraction of dry mass partitioned to fruits (F_{fruits}) decreased with the increase in PPFD from 300 to 700 µmol m^{-2} s^{-1} (Figure 3.5). The FBRUE and RUE under 300 µmol m^{-2} s^{-1} PPFD were the highest. The integrated PPFD received by the plant until 82 DAS (I_{PPFD}), total dry weight (W), fruit dry weight (W_{fruits}), and the difference between the PPFDs at the top and bottom of the plant

($PPFD_T$) increased with an increase in PPFD from 300 to 700 μmol m^{-2} s^{-1}. PPFD significantly affected F_{fruits}, W, W_{fruits}, $PPFD_T$, and average PLA (Table S3.2). Higher PPFD led to lower FBRUE because of lower RUE and F_{fruits} from 300 to 700 μmol m^{-2} s^{-1} (Figure 3.5). The decrease in RUE was greater than that in F_{fruits} in the three treatments. The reason for the decrease in RUE with an increase in PPFD was that the increase in W was less than the increase in I_{PPFD}.

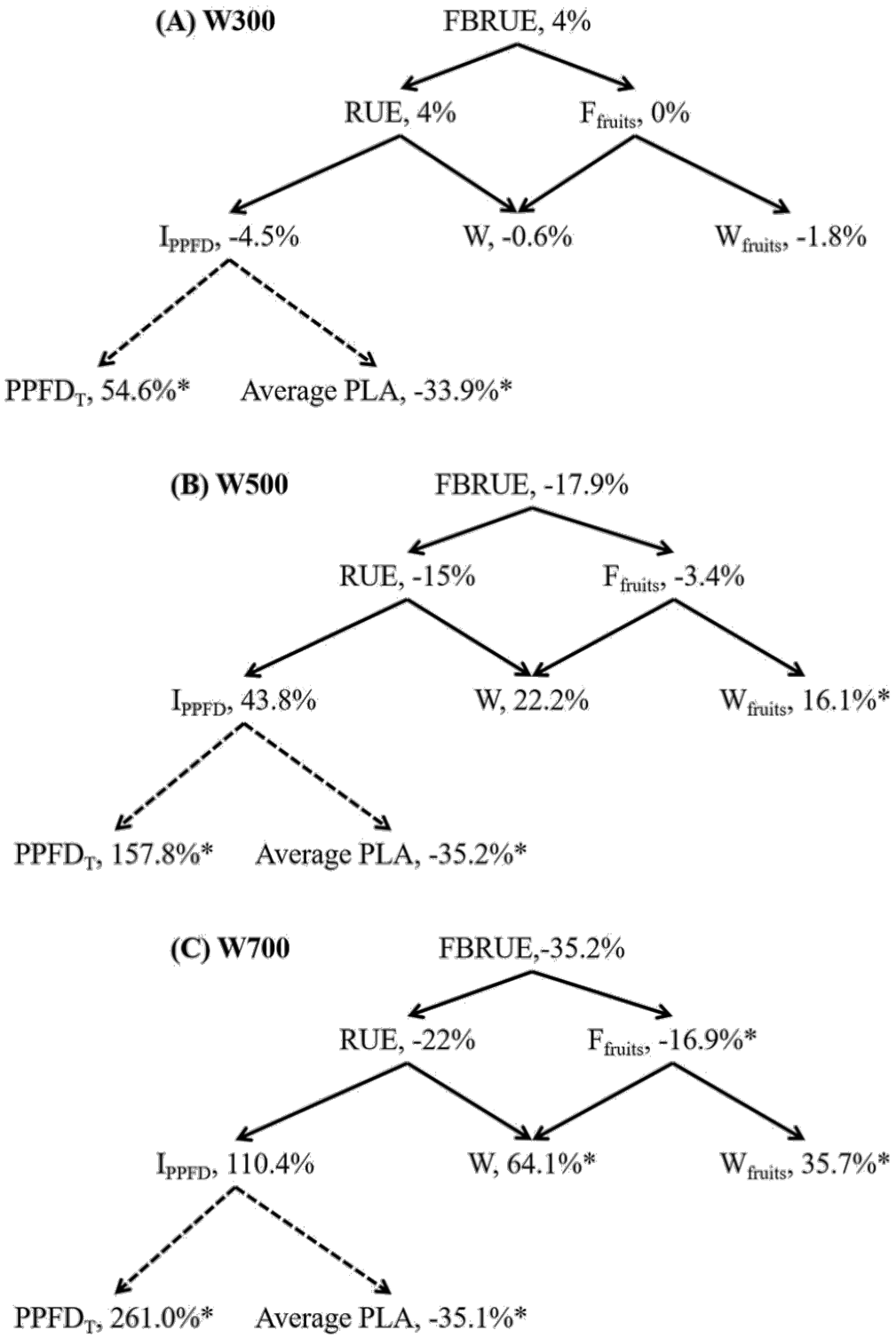

Figure 3.5 Fruit biomass radiation-use efficiency (FBRUE) component analyses under 300 (A), 500 (B), 700 (C) μmol m^{-2} s^{-1} PPFDs at 82 DAS. The asterisks indicate significant differences among treatments based on Tukey−Kramer's test at $*p < 0.05$ (n = 3−4). For black solid arrows, the arrowhead component is used to calculate the parent parameter in the tail. For black dotted arrows, the arrowhead component is affected by

the tail component. Percentages are the increment relative to W200; all values in W200 are considered 100%. Abbreviations within schemes are as follows: FBRUE, fruit biomass radiation-use efficiency, g mol^{-1}; RUE, radiation-use efficiency, g mol^{-1}; F_{fruits}, fraction of dry mass partitioned to fruits, g g^{-1}; I_{PPFD}, integrated PPFD received by the plant until 82 DAS, mol; W, total dry weight, g; W_{fruits}, fruit dry weight, g; $PPFD_T$, difference between the PPFDs at the top and bottom of the plant, mol m^{-2} s^{-1}; Average PLA, average projected leaf area, m^2. All sampled plants are NP plants.

Figure 3.5A shows that the difference in FBRUE between W200 and W300 was small because of the small differences in RUE and F_{fruits} between W200 and W300. The average PLA decreased by 33.9%, and there was a 4.5% decrease in the I_{PPFD} when the PPFD at the top of the canopy increased from 200 to 300 μmol m^{-2} s^{-1}. The $PPFD_T$ and average PLA in W300 were significantly higher and lower, respectively, than those in W200. $PPFD_T$ and W_{fruits} in W500 were significantly higher than those in W200 (Figure 3.5B). The average PLA in W500 was significantly lower than that in W200. $PPFD_T$ and W_{fruits} in W700 were significantly higher than those in W200 (Figure 3.5C). The F_{fruits} and average PLA in W700 were significantly lower than those in W200.

FBRUE increased rapidly and then flattened in all treatments (Figure 3.6). At 71 DAS, the FBRUE values in W200 and W300 were higher than those in W500 and W700. Finally, the FBRUE increased slightly as the PPFD increased from 200 to 300 μmol m^{-2} s^{-1}, decreased as the PPFD increased from 300 to 700 μmol m^{-2} s^{-1}, and was the highest in W300 at 82 DAS.

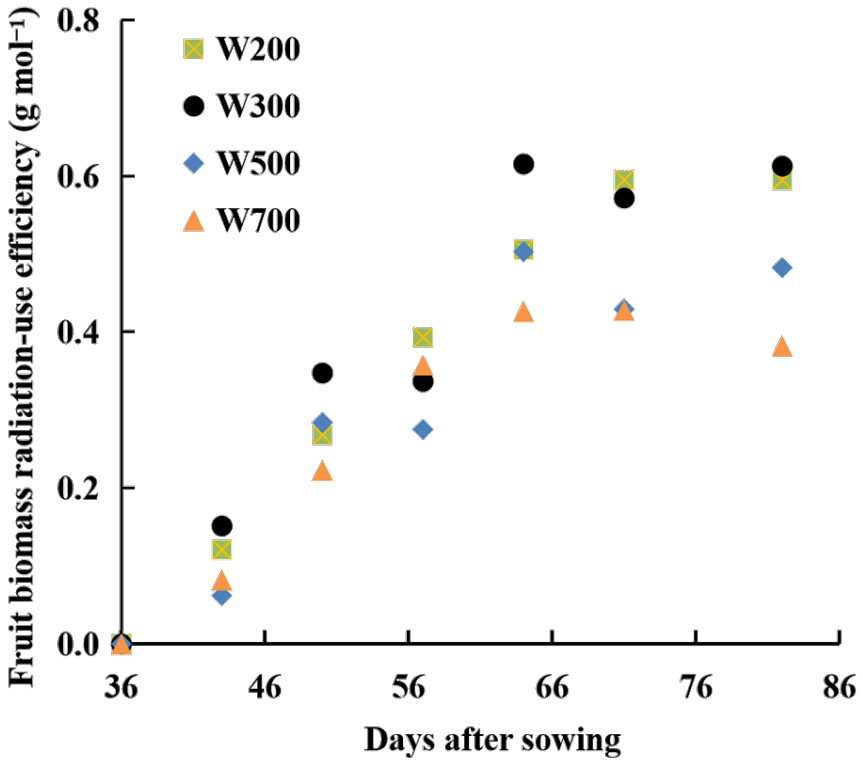

Figure 3.6 Effect of PPFD on fruit biomass radiation-use efficiency (FBRUE) over time in 'Micro-Tom'. All sampled plants are NP plants.

3.3.6. Dry mass partitioning to fruits, yield, and fruit quality

The F_{fruits} increased from 36 DAS to 64 DAS in all treatments and remained stable from 0.49 to 0.60 until 82 DAS (Figure 3.7). At 57 DAS, F_{fruits} in W500 were significantly higher than those in W200 and W300. At 64 DAS, the F_{fruits} under 300 µmol m^{-2} s^{-1} PPFD were the highest among all treatments and were significantly higher than that under 200 µmol m^{-2} s^{-1} PPFD. In addition, it was significantly higher in W200 than that in W500 at 71 DAS. Finally, it was lowest under 700 µmol m^{-2} s^{-1} PPFD at 82 DAS. In addition, the F_{fruits} were the largest and the fraction of dry mass partitioned to stems was the lowest among all organ fractions in all treatments at 50 DAS (Figure S3.4).

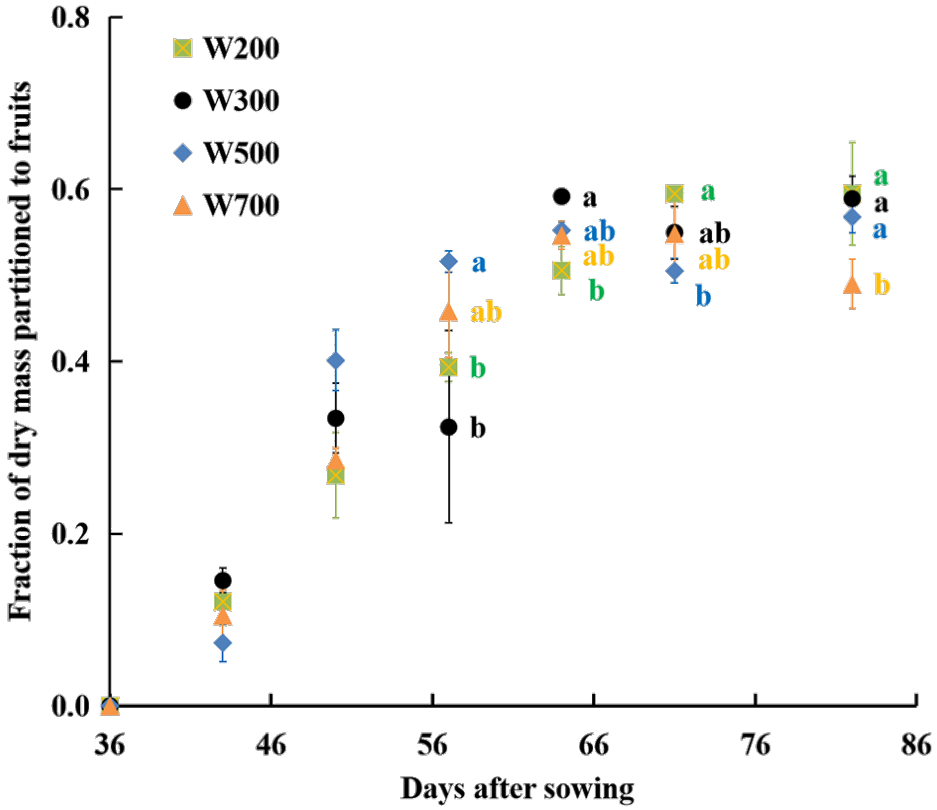

Figure 3.7 Effect of PPFD on the fraction of dry mass portioned to fruits (F_{fruits}) over time in 'Micro-Tom'. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ ($n = 3$−4). All sampled plants are NP plants.

The number of fruits, fresh fruit, and dry weight increased with an increase in PPFD (Table 3.4). In W700, they were significantly higher than those in the other three treatments at 82 DAS. The number of fruits in W300 and W500 was significantly higher than those in W200. The fresh and dry weights of the fruits in W200 and W300 were significantly lower than those in W500 and W700. There were no significant differences in the fruit dry matter ratio or Brix among the treatments. Brix/acidity increased, and acidity decreased with an increase in PPFD. Brix/acidity was significantly higher, and acidity was significantly lower in W700 than in W200.

Table 3.4 Effects of PPFD on the number of fruits, fruit fresh and dry weight, fruit dry matter ratio, and fruit quality in Micro-Tom 82 DAS. Each value represents the mean ± standard error. Different letters indicate significant differences at the $p < 0.05$ level among PPFD treatments with Tukey−Kramer's test. Each value of the number of fruits, fruit fresh and dry weight, and fruit dry matter ratio represents a mean of three or four values. There were 7−8 fruits sampled in each treatment for fruit quality. All sampled plants are NP plants.

Treatment	Number of fruits	Fruit fresh weight (yield, g)	Fruit dry weight (g)	Fruit dry matter ratio (%)	Brix (%)	Acidity (%)	Brix/acidity
W200	10.6 ± 1.2 c	67.73 ± 6.54 c	6.53 ± 0.70 c	9.33 ± 0.33	5.61 ± 0.38	1.31 ± 0.14 a	4.55 ± 0.51 b
W300	14.3 ± 0.6 b	66.76 ± 10.44 c	6.41 ± 1.05 c	9.75 ± 0.25	5.73 ± 0.35	1.29 ± 0.06 ab	4.48 ± 0.31 b
W500	15.0 ± 1.4 b	80.33 ± 4.88 b	7.58 ± 0.56 b	9.25 ± 0.25	5.99 ± 0.21	1.09 ± 0.06 ab	5.55 ± 0.25 ab
W700	17.4 ± 1.6 a	90.70 ± 7.20 a	8.86 ± 0.83 a	9.75 ± 0.25	6.61 ± 0.19	0.99 ± 0.08 b	6.98 ± 0.62 a

3.3.7. Source strength and fruit sink strength

The total dry weight of a plant (W) increased with time and PPFD (Figure 3.8). The fitted curves followed an exponential function, and the R^2 values for all treatments exceeded 0.8. The same trend as W was observed in the source strength (S_{source}) (Figure 3.9). S_{source} was lowest under 200 μmol m^{-2} s^{-1} PPFD and highest under 700 μmol m^{-2} s^{-1} PPFD at all times among all treatments.

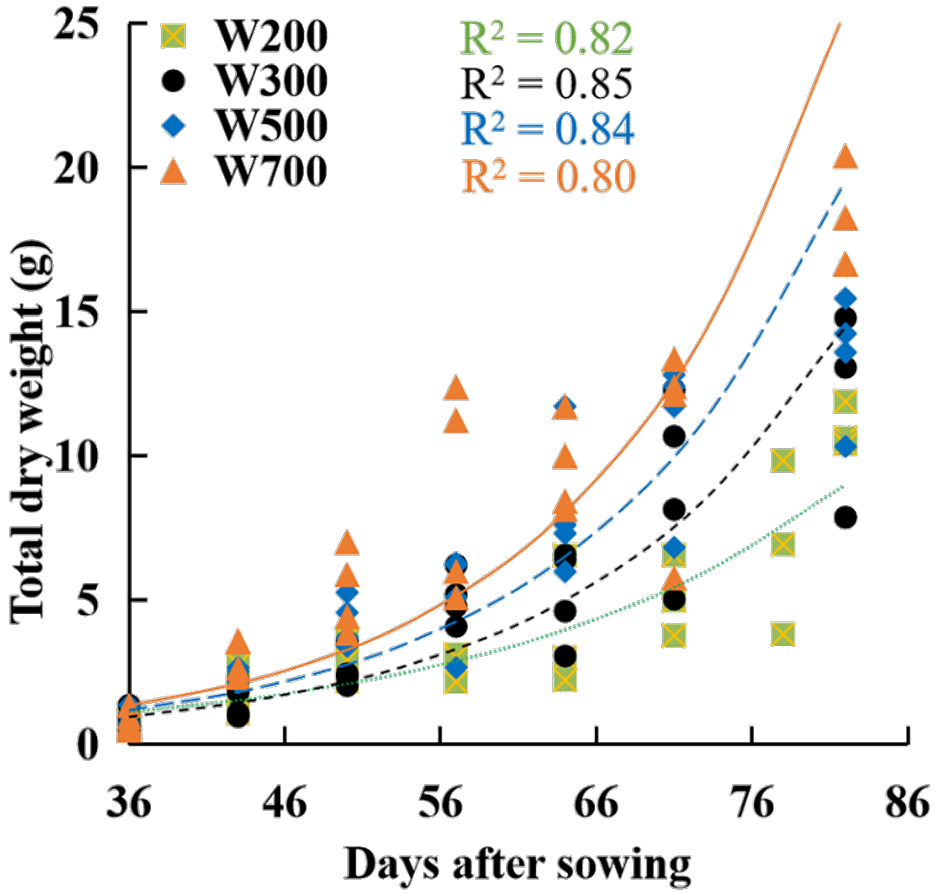

Figure 3.8 Effect of PPFD on the total dry weight of a plant over time in 'Micro-Tom'. Symbols represent measured total dry weights in W200(▣), W300 (●), W500 (◆), and W700 (▲). Curves represent exponential function fitted for W200 (·····), W300 (----), W500 (– –), and W700 (——). R^2 is coefficient of determination in W200 (green), W300 (black), W500 (blue), and W700 (orange), respectively. All sampled plants are NP plants.

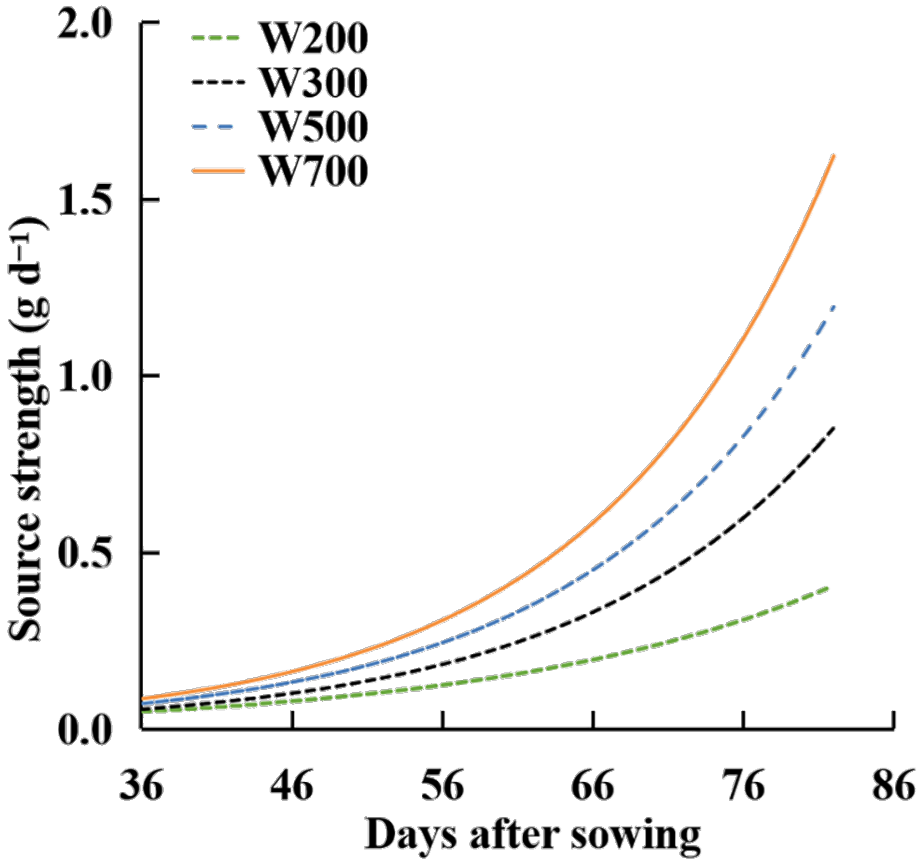

Figure 3.9 Effect of PPFD on source strength (S_{source}) over time in 'Micro-Tom' with standard fruit load (no fruit pruned).

There were no significant differences in fruit volume and single fresh and dry weights between one-fruit (OFP) plants and one-fruit per truss (OFT) plants in W300, W500, and W700 (Table S3.3). The relationships between fresh fruit weight and fruit volume of OFP were well fitted with linear regression without intercept ($R^2 > 0.97$ for all fits, shown in Figure S3.2) in the three treatments. The fresh weight ratios to fruit volume in W300, W500, and W700 were 1.047, 1.020, and 1.016 g cm^{-3}, respectively. Moreover, the ratio of fresh weight to fruit volume of NP plants was similar to that of the OFP plants (Figure S3.2). As a result, this study assigned the ratio of fresh weight to fruit volume to 1.0 g cm^{-3}. Specifically, PPFD had little effect on the ratio of fresh weight to fruit volume in 'Micro-Tom.' All data for fruit volume (12 fruits) in the three treatments are shown in Figure 3.10A because there was no significant difference in fruit volume among the three treatments. The fresh weight of the potentially growing

fruits (Figure 3.10B) was estimated using the calculated fruit volume (Figure 3.10A).

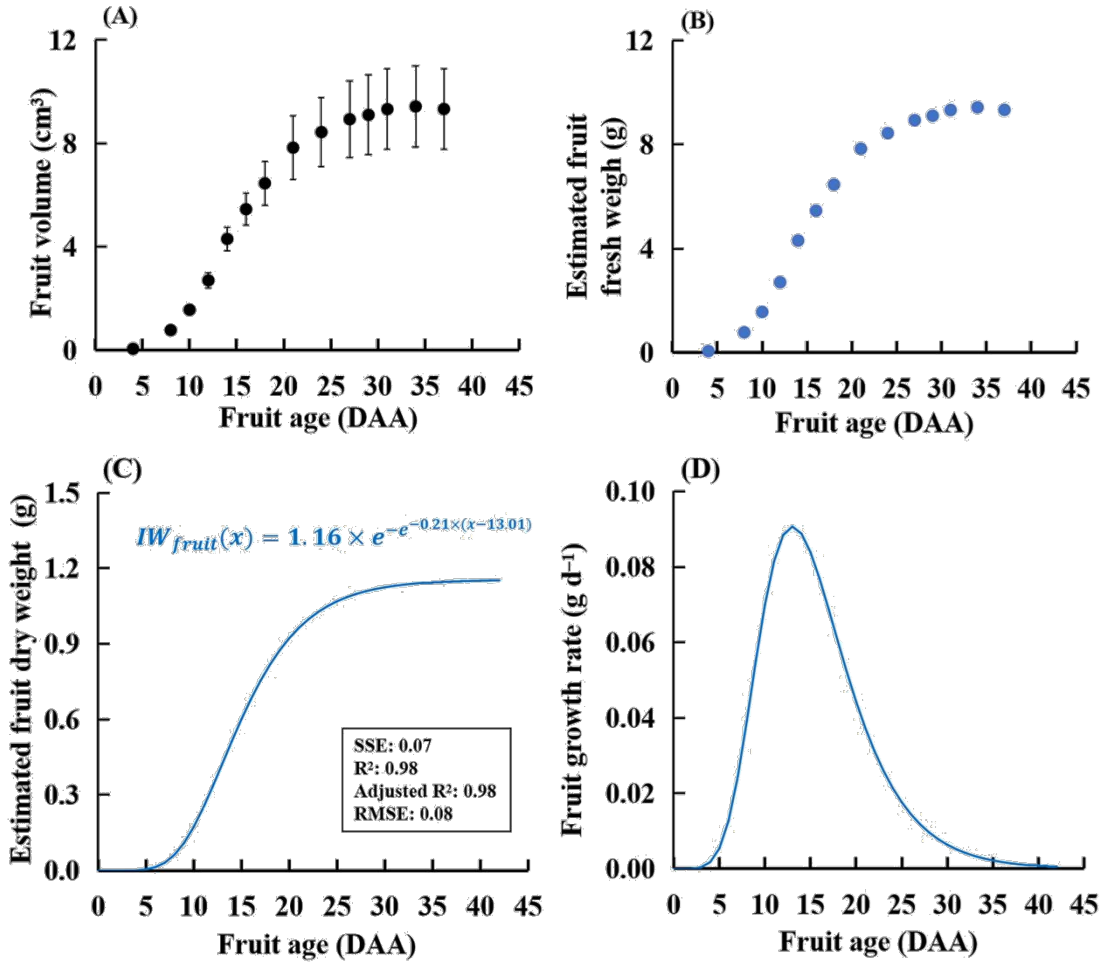

Figure 3.10 Calculated volumes (A, by measuring fruit diameters and heights in one-fruit plants), estimated fresh weight (B), estimated dry weight (C), and fruit growth rate (D) of an individual fruit with potential growth over time in 'Micro-Tom'. The sample size in (A) was 12. Estimated dry weight (C) is $IW_{fruit}(x)$ in Equation 3-7. Fruit growth rate in (D) is $IGR_{fruit}(x)$ in Equation 3-8.

There was no significant difference in fruit dry matter content among W300, W500, and W700 plants (data not shown). The fruit dry matter content in the OFP plant as a function of fruit age in the three treatments is shown in Figure S3.5. Changes in fruit dry matter content with time among the three PPFD treatments were slight during days 9–42 after anthesis (DAA). The goodness of fit parameters in the OFP plant were calculated and are shown in Figure S3.5. Finally, the 4th-degree polynomial function (Equation 3-6) was as follows:

$IDMC_{fruit}(x) = -3.12 \times 10^{-5} \times x^4 + 2.482 \times 10^{-3} \times x^3 - 5.957 \times 10^{-2} \times x^2 + 0.374 \times x + 14.31$

where x is the DAA and $IDMC_{fruit}(x)$ is the fruit dry matter content (%) at x DAA.

This function estimated the fruit dry matter content at different DAA. The estimated dry weight (Figure 3.10C) and growth rate of each fruit (Figure 3.10D) over time were determined according to Equations 3-7 and 3-8. The maximum dry weight of the fruit (IW_{fruit}) was 1.16 g. The growth rate coefficient (k) and fruit age at the maximum growth rate (x_m) were 0.21 and 13 DAA Equation 3-7.

The fruit sink strength ($S_{fruit\text{-}sink}$) in all treatments showed a rising to declining trend over time (Figure 3.11). The peaks of the $S_{fruit\text{-}sink}$ increased with an increase in PPFD. Until 60 DAS, $S_{fruit\text{-}sink}$ decreased with the decrease in PPFD and was the lowest in the W200 treatment among all treatments. The $S_{fruit\text{-}sink}$ in the W200 treatment was the highest, from 63 to 82 DAS.

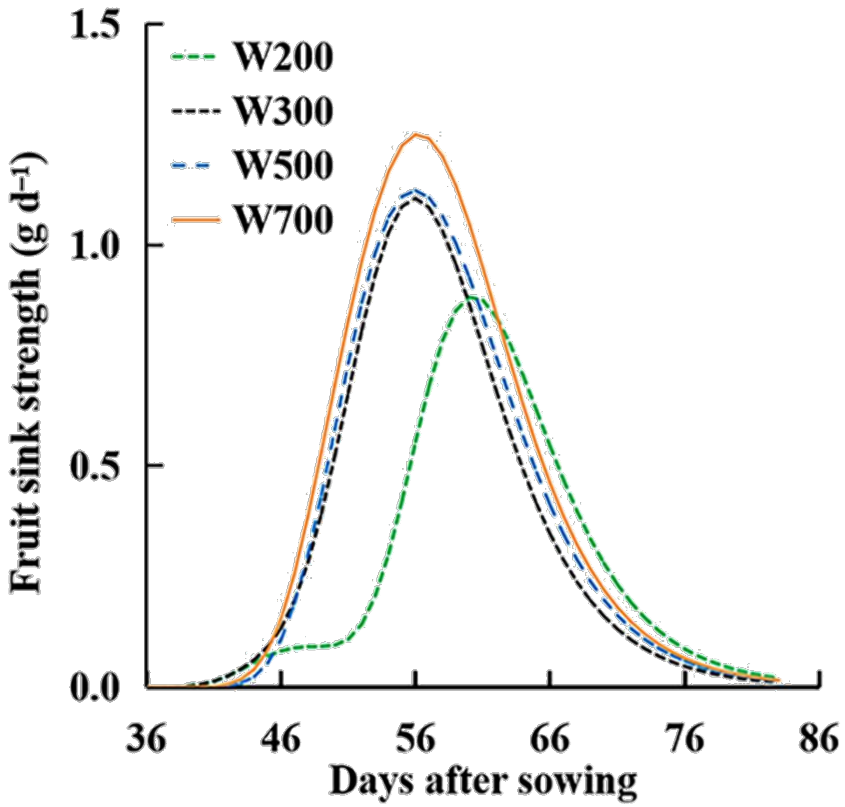

Figure 3.11 Effect of PPFD on fruit sink strength ($S_{fruit\text{-}sink}$) over time in 'Micro-Tom' with standard fruit load (no fruit pruned).

3.3.8. Light electric energy productivity

Higher PPFD led to higher power of lamps and light electric energy consumption during a growth cycle but lower light electric energy productivity (Table 3.5). Light electric energy productivity in W200 was 1.5 times that in W700.

Table 3.5 E ffects of PPFD on power of lamps during experiments, light electric energy consumption during a growth cycle and light electric energy productivity in 'Micro-Tom' 82 DAS. FW is fresh weight of fruits (g).

Treatment	Power of lamps during experiments (W/m^2 ground area[x])	Light electric energy consumption during a growth cycle[y] (MJ/m^{-2} ground area)	Light electric energy productivity[z] (g FW/MJ)
W200	96.6	545.6	42.7
W300	144.9	676.3	31.3
W500	193.2	807.0	29.9
W700	241.5	937.8	28.1

[x]Ground area is defined as the cultivation area under 8 lamps used in each treatment, which is 0.6 m × 1.3 m = 0.78 m^2.
[y]A growth cycle is 0−82 DAS in 'Micro-Tom'.
[z]Light electric energy productivity (Kozai, 2018) is the yield of tomatoes (g) per unit electric energy consumption for lighting (MJ).

3.4. Discussion

3.4.1. Growth and biomass production

'Micro-Tom', a dwarf tomato, is known to grow, set, and ripen fruit even at extremely low light levels (photosynthetic photon flux density (PPFD):100 μmol m^{-2} s^{-1}; daily light integral (DLI): 5.76 mol m^{-2} d^{-1}) (Frantz et al., 2000). In addition, according to a study by Kato et al. (2011), at a PPFD of 400 μmol m^{-2} s^{-1} and a CO_2 concentration of 500 μmol mol^{-1}, the net photosynthetic rate (Pn) of Cross no. 2 plants (transgenic tomato bred by cross-breeding line 56B and 'Micro-Tom') was saturated. However, few studies have reported whether a high PPFD can inhibit biomass production and plant height in 'Micro-Tom.' There is evidence that a commercial tomato culture requires a minimum of 30 mol m^{-2} d^{-1} of light integral, and a light integral of 4.8–6.0 mol m^{-2} d^{-1} is generally considered optimal for tomato seedling production (Heuvelink and Dorais, 2018). Monthly averaged DLI values range from 20 to 40 mol m^{-2} d^{-1} in the tropics to 15 and 60 mol m^{-2} d^{-1} at a latitude of 30° (Poorter et al., 2019). Glass and other greenhouse structures absorb or reflect 30–70% of the external light in greenhouses. Thus, the DLI levels in greenhouses rarely exceeded 30 mol m^{-2} d^{-1}. The most common DLIs in growth chambers are between 10 and 30 mol m^{-2} d^{-1} (Poorter et al., 2016). In this study, the DLIs of W200, W300, W500, and W700 were 11.52, 17.28, 28.80, and 40.32 mol m^{-2} d^{-1}, respectively. Therefore, a DLI of 40.32 mol m^{-2} d^{-1} is high, even for general tomato cultivars.

Compared with those under 200 and 300 μmol m^{-2} s^{-1} PPFD, the total fresh and dry weights and the total dry matter ratio were significantly higher under 700 μmol m^{-2} s^{-1} PPFD (Table 3.2). Therefore, 700 μmol m^{-2} s^{-1} PPFD (DLI, 40.32 mol m^{-2} d^{-1}) did not inhibit biomass production until 82 DAS.

PPFD can affect the plant height and stem length in some tomato cultivars. Cherry tomato seedlings (*Solanum lycopersicum* cv. Mill qianxi) decreased in height as the PPFD increased from 50 to 500 μmol m^{-2} s^{-1} (Fan et al., 2013). The stem length of the tomato cultivar 'Momotaro Fight' at a PPFD of 150 μmol m^{-2} s^{-1} was significantly

longer than that at a PPFD of 300 μmol m^{-2} s^{-1} in a study by Matsuda et al. (2016). Under different experimental conditions, different species and cultivars may respond differently to the PPFD. As a result of the present experiment, no significant differences were observed in the height of plants under different PPFD treatments (Table 3.2), which was similar to the result at the vegetative growth stage (Ke et al., 2021), probably because the cultivar 'Micro-Tom' is a dwarf tomato.

3.4.2. RUE, light absorption, ϕ, and P_{max}

Light is one of the limiting resources in natural conditions, and plants grown under low PPFD conditions are required to adapt to capture light effectively (Lee and Graham, 1986). Conversely, leaves grown under low PPFD conditions have thicker cuticles and higher SLA and chlorophyll concentrations than those grown under high PPFD conditions (Araus and Hogan, 1994). Under high PPFD, leaves had higher reflectance and lower transmittance and absorptance than those under low PPFD (Table 3.3). Low absorptance under high PPFD could cause the integrated PPFDs received by the plant (I_{PPFD}) to be overvalued and radiation-use efficiency (RUE) to be undervalued.

In addition, plants are exposed to excessive amounts of light over a long period, producing large amounts of reactive oxygen species, superseding the antioxidant system, and resulting in irreversible photooxidative damage to chloroplasts and cells, thus preventing photosynthesis (Karpinski et al., 1997). A PPFD of 700 μmol m^{-2} s^{-1} might have been too high to decrease the photosynthetic quantum yield (ϕ) (Figure 3.3E and F), and the photosynthetic capacity of the leaves (Figure 3.3I) did not inhibit biomass production. This decrease and inhibition became more significant over time (Figure 3.3). Higher PPFD led to lower ϕ at PPFDs of 200, 300, 500, and 800 μmol m^{-2} s^{-1} at 64 DAS (Figure 3.3E and F), which was the main reason high PPFD led to low RUE (Figure 3.4).

The growth stage can affect RUE. The RUEs in W300, W500, and W700 at the vegetative growth stage were 1.15, 1.14, and 0.94 g mol^{-1}, respectively (Ke et al., 2021). However, the RUEs in W300, W500, and W700 at the reproductive growth stage were

1.04, 0.85, and 0.78 g mol^{-1}, respectively. The RUE during the reproductive growth stage was lower than that during the vegetative growth stage, even in the same cultivation environment. One reason might be that the leaf age at the vegetative growth stage was younger than that at the reproductive growth stage. As a determinate tomato, 'Micro-Tom' plants stop shoot production on the main stem once flowering. The top leaves on the stem became older because no new leaves appeared on the main stem. In addition, the net leaf photosynthetic rate (Pn) decreased over time at the same PPFD (Figure 3.3A, B, and C). Another reason is that the fruit was set on the top canopy and part of the light was illuminated and absorbed by the fruits. The gross photosynthetic rate per green fruit surface area is only 15–30% of the rate per leaf area (Czarnowski and Starzecki, 1990). Therefore, RUE decreased with the growth of fruit set in the canopy.

The RUE in W300 (1.04 g mol^{-1}) was the highest (Figure 3.4). Therefore, 300 μmol m^{-2} s^{-1} PPFD was recommended for 'Micro-Tom' cultivation at the reproductive growth stage to improve RUE. Furthermore, Ke et al. (2021) reported that 300 μmol m^{-2} s^{-1} PPFD was proposed for 'Micro-Tom' cultivation during the vegetative growth stage to enhance the RUE. Therefore, 300 μmol m^{-2} s^{-1} PPFD can be applied to 'Micro-Tom' cultivation during vegetative and reproductive growth stages to enhance RUE.

3.4.3. FBRUE and the fraction of dry mass portioned to fruits

Fruit biomass radiation-use efficiency (FBRUE) decreased because RUE and the fraction of dry mass partitioned to fruits (F_{fruits}) decreased with an increase in PPFD from 300 to 700 μmol m^{-2} s^{-1} (Figure 3.5). The decrease in RUE was larger than that in F_{fruits}, and PPFD affected RUE more than F_{fruits}. The influence of PPFD on F_{fruits} increased with an increase in the PPFD. Until 56 DAS, RUE had a greater influence on FBRUE than F_{fruits} because there was no significant difference in F_{fruits} among all treatments (Figure 3.7). From 56 DAS onwards, the impact of PPFD on F_{fruits} had a greater influence on FBRUE (Figures 3.6 and 7). Previous studies reported that the FBRUE of tomatoes cultivated in the same controlled environment agriculture systems

at harvest was 0.2−0.36 g mol^{-1} (Wheeler et al., 2008; Goto, 2011; Li et al., 2019). In the present study, even the lowest FBRUE at harvest in W700 was 0.38 g mol^{-1} (Figure 3.6 and Table S3.2) which was higher than others. This shows that the environmental control and variety selection used in the present study improved the FBRUE of tomatoes.

The F_{fruits} increased from 36 DAS to 64 DAS and remained stable, ranging from 0.49 to 0.60 at harvest. Generally, the F_{fruits} (not including root dry mass) of year-round greenhouse indeterminate tomatoes was 69–72% (Cockshull et al., 1992; De Koning, 1993). For field-grown semi-determinate tomatoes, F_{fruit} (excluding root dry mass) was 53–71%, with an average of 58% (Scholberg et al., 2000), and for processing tomatoes, it ranged from 57 to 67%. (Cavero et al., 1998; Hewitt and Marrush, 1986). In the present study, the fraction of dry mass partitioned to the root was approximately 10% (Figure S3.4); therefore, the F_{fruits} (not including root dry mass) in the present study was 56–65%, which is similar to the values reported in previous studies.

In addition, fruit dry weight increased by 16.1% and 35.7% when PPFD at the top of plants increased by 157.8% (W500) and 261.0% (W700), respectively, from 200 μmol m^{-2} s^{-1} (Figure 3.5B and C). In practice, the 'one-percent rule' is often used to estimate the impact of light on the production, stating that an increase in light by 1% will result in an increase in production by 1%. For tomatoes, this value varies between 0.7% and 1% (Marcelis et al., 2006). However, 'Micro-Tom' is a determinate tomato cultivar that is different. However, the number of fruits on the main stem is limited. Therefore, the fruit sink strength is limited. This might be why the F_{fruits} decreased with an increase in PPFD in the present study, while the F_{fruits} of indeterminate tomatoes increased with an increase in PPFD (Yan et al., 2018).

Higher PPFD led to lower light electric energy productivity and the light electric energy productivity in W200 was higher than that in W300 (Table 3.5). This was because that the fresh weight of fruits per plant, which was the numerator, in W200 was almost same with that in W300 (Table 3.4). However, the light electric energy consumption per ground area, which was the denominator, in

W300 was 1.5 times that in W200 (Table 3.6).

3.4.4. Source strength and fruit sink strength

The total dry weight of a plant (W, Figure 3.8) and the source strength (S_{source}, Figure 3.9) increased with an increase in PPFD. However, F_{fruits} did not increase with an increase in PPFD from 56 DAS. This means that the dry mass produced was transferred more to leaves and roots than to the target organ fruits at high PPFDs (Figure S3.4). The main reason was that the fruit sink strength ($S_{fruit\text{-}sink}$, Figure 3.11) decreased from 56 DAS at high PPFDs. Two factors can directly affect the $S_{fruit\text{-}sink}$: sink strength of each single fruit (potential growth rate of individual fruit, IGR_{fruit}) and the number of fruits. PPFD did not affect the potential growth rate of individual fruits (Figure 3.10D) in 'Micro-Tom,' which was similar to a previous study (Marcelis, 1996). However, the number of fruits and the peak of $S_{fruit\text{-}sink}$ increased with an increase in PPFD (Figure 3.11).

High PPFD is necessary at the early reproductive growth stage to induce flower bud differentiation and improve the number of flowers (Samach and Lotan, 2007) and fruit sink and yield. This also resulted in a high PPFD, increasing the Brix and Brix/acidity (Table 3.4), indicating better fruit quality under high PPFD. Generally, starch, particularly in the columella, placenta, and inner and radial pericarps (Schaffer and Petreikov, 1997), is filled in the early phase of fruit expansion and peaks around 10–25 DAA (Bertin et al., 2009). Maximum starch levels correlate well with the final levels of soluble sugars (Ho, 2003). In indeterminate tomatoes, the $S_{fruit\text{-}sink}$ was initially low and soon increased to a plateau and remained constant until 100 days after planting (Li et al., 2015). However, high PPFD and S_{source} might not be necessary for 'Micro-Tom' at the late reproductive growth stage (from 64 DAS), when F_{fruits} (Figure 3.7) was stable and $S_{fruit\text{-}sink}$ (Figure 3.11) was low. Because there were no new fruits on the main stem at the late reproductive growth stage, dynamic PPFD management, high PPFD before 64 DAS, and low PPFD from 64 DAS might be suitable for improving FBRUE, yield, and fruit quality in 'Micro-Tom' at the reproductive growth stage.

3.5. Conclusions

Our study showed that FBRUE increased slightly with an increase in PPFD from 200 to 300 μmol m^{-2} s^{-1} and decreased because of the decreases in RUE and F_{fruits} when PPFD increased from 300 to 700 μmol m^{-2} s^{-1}. From 300 to 700 μmol m^{-2} s^{-1} PPFD, higher PPFD led to lower RUE because of lower ϕ and P_{max}. In addition, S_{source} and $S_{fruit\text{-}sink}$ increased with an increase in PPFD. PPFD did not affect the potential growth rate of individual fruits but the number of fruits. Therefore, 300 μmol m^{-2} s^{-1} PPFD is recommended for 'Micro-Tom' cultivation to improve FBRUE and RUE at the reproductive growth stage. A PPFD of 700 μmol m^{-2} s^{-1} is recommended for 'Micro-Tom' cultivation to improve yield and fruit quality. Furthermore, dynamic PPFD management based on the source-sink relationship might be suitable for improving FBRUE, yield, and fruit quality in 'Micro-Tom' during the reproductive growth stage. The results of this study would be helpful in efficient tomato production in PFALs and may help elucidate the effects of PPFD on FBRUE, source strength, and fruit sink strength of dwarf tomatoes under the LED light. In addition, the light quality is also key consideration for improvement of RUE and FBRUE. Further research is necessary for detecting the optimal combination of PPFD and light quality to enhance RUE and FBRUE in dwarf tomatoes.

3.6. Supplementary materials

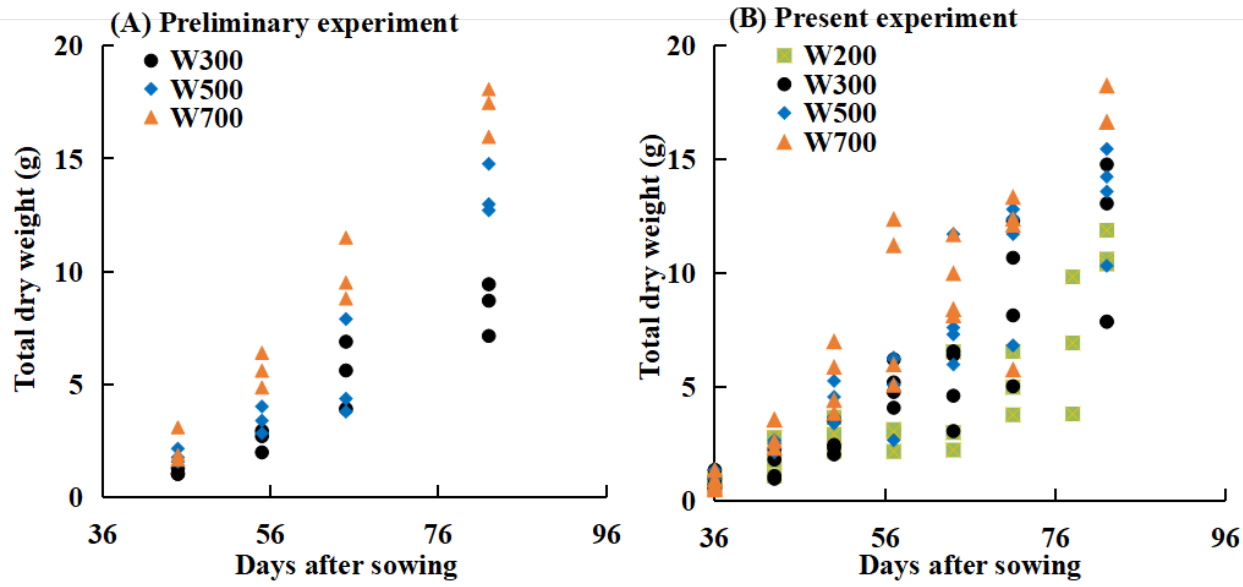

Figure S3.1. The total dry weight of a 'Micro-Tom' plant from 36 to 84 days after sowing (DAS) in different photosynthetic photon flux density (PPFD) treatments in a preliminary experiment (A) and present experiment (B).

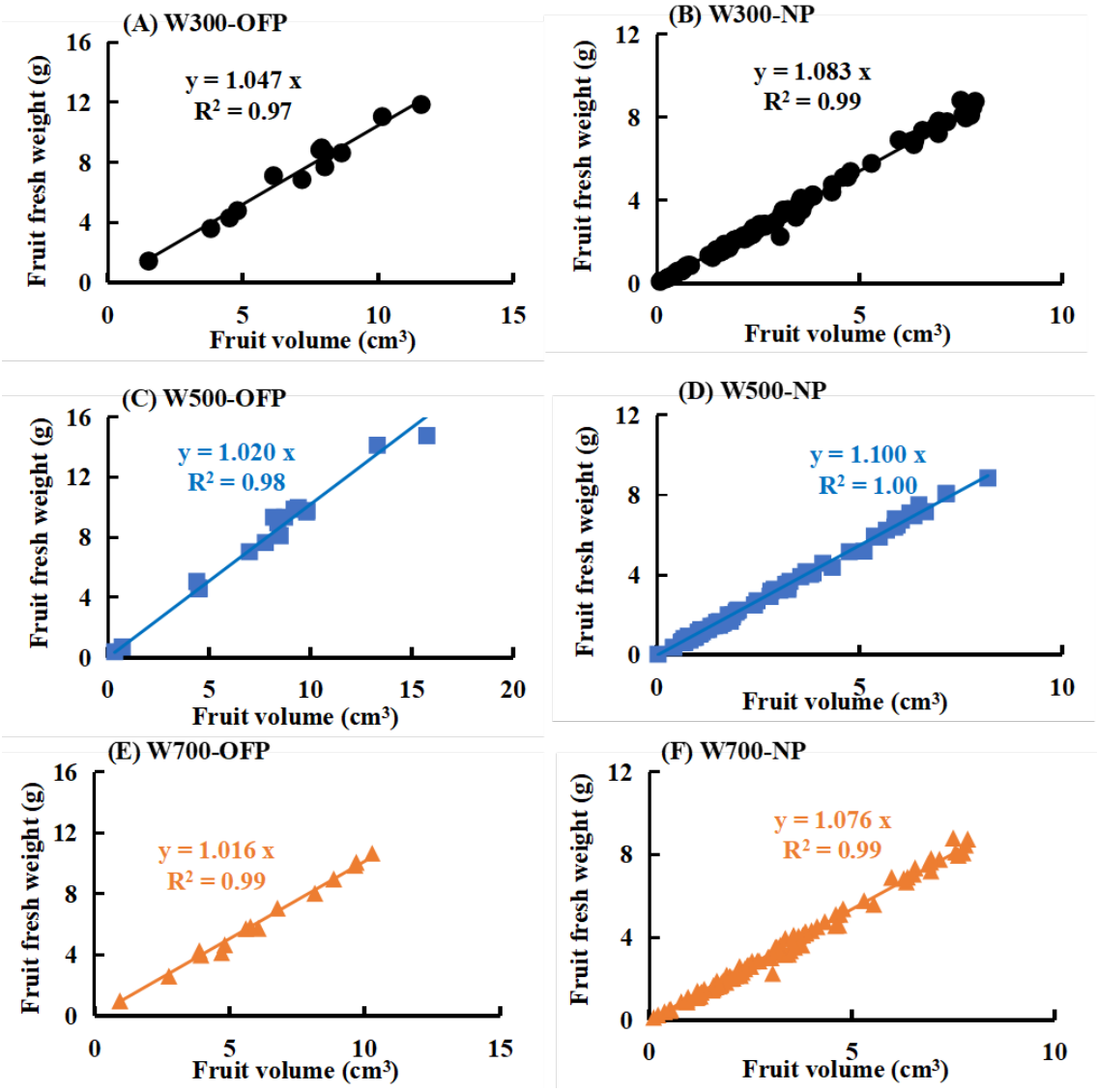

Figure S3.2. The relationships between individual fruit fresh weight and volume of one-fruit plants (OFPs) (A) and plants without fruit pruning (NPs) (B) in W300, of OFPs (C) and NPs (D) in W500, and OFPs (E) and NPs (F) in W700. There were 15–16 fruits of OFPs, and 77–104 fruits of NPs sampled in each PPFD treatment.

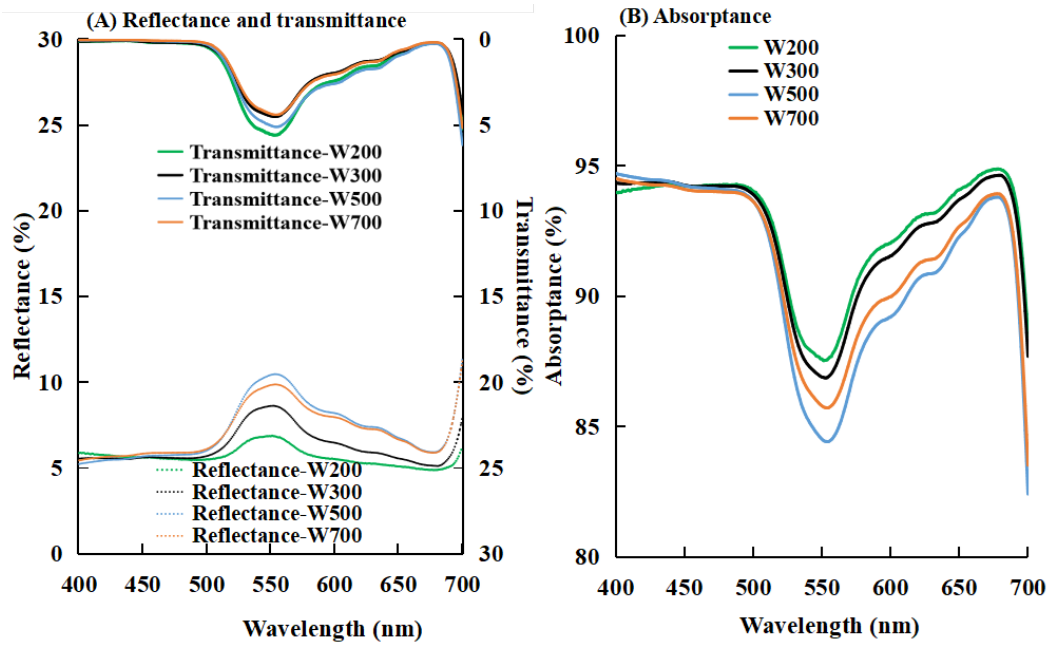

Figure S3.3. Effects of PPFD on the spectra of reflectance and transmittance (A) and absorptance (B) of leaves in 'Micro-Tom' 82 DAS. The range of measured light spectrum was 400–700 nm. W200, W300, W500, and W700 denote 200, 300, 500, and 700 µmol m^{-2} s^{-1} PPFD, respectively. Each value represents the average of the values of four NPs.

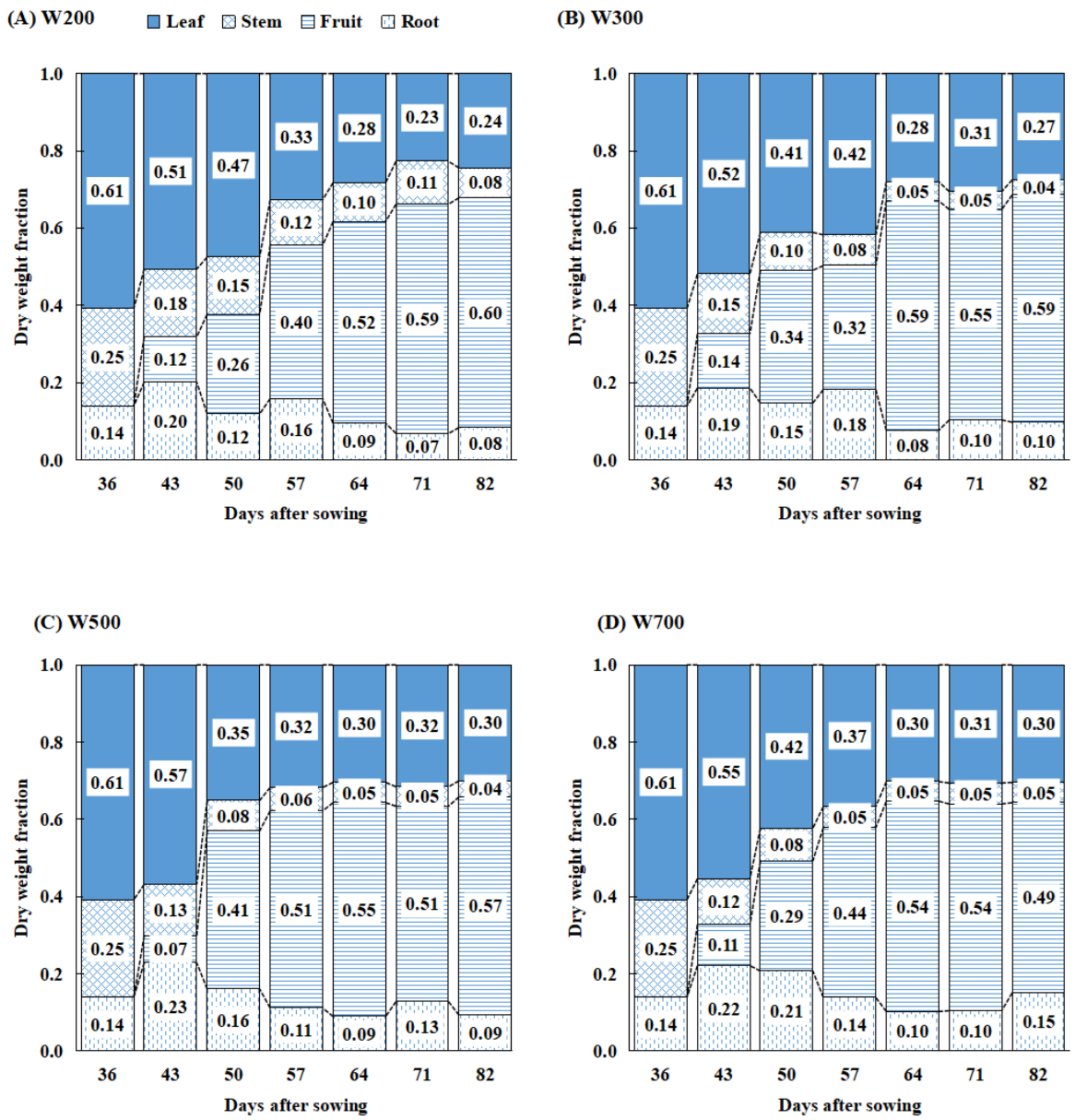

Figure S3.4. Fractions of dry mass partitioned to each organ in W200 (A), W300 (B), W500 (C), and W700 (D) treatments in 'Micro-Tom' 36, 43, 50, 57, 64, 71, and 82 days after sowing (DAS). Each value represents the mean of three or four values. All sampled plants are NPs.

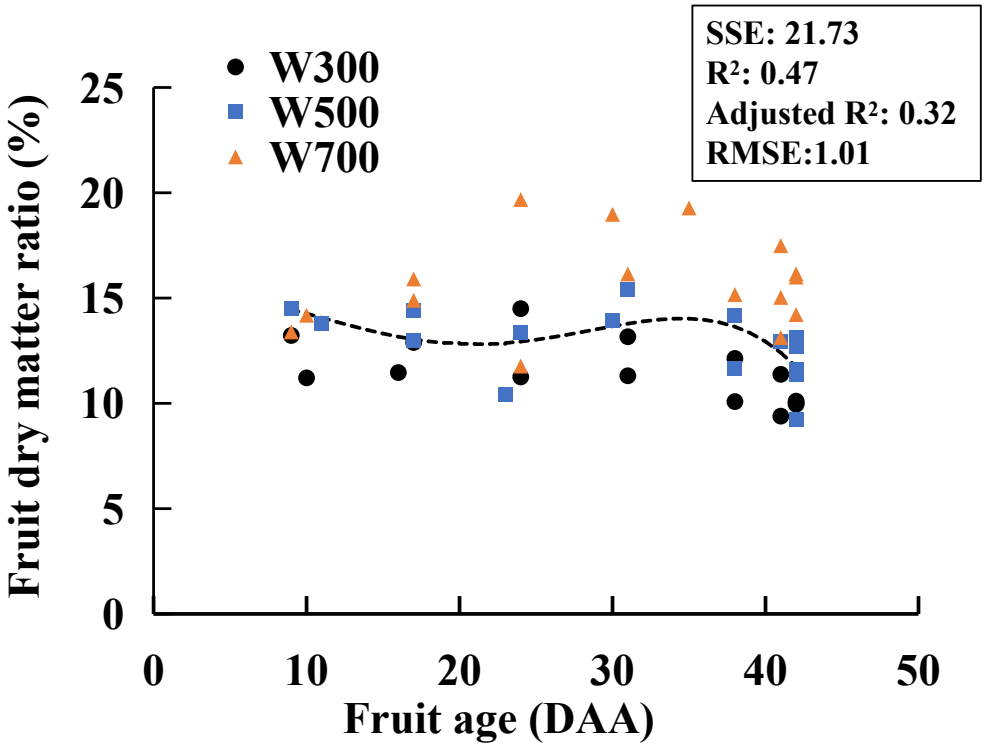

Figure S3.5. The relation between fruit age and dry matter content of one-fruit plants (OFP) in W300, W500, and W700 treatments. There were 11–15 fruits sampled in each PPFD treatment. Curves represent the 4th-degree (or 3rd-degree) polynomial function used to fit the data in the three treatments (Equation 6). Goodness of fit of fitted curves are shown in the box. SSE, R^2, adjusted $R^{2,}$ and RMSE represent the sum of squares due to error, coefficient of determination, degree-of-freedom adjusted coefficient of determination, and root mean squared error, respectively.

Table S3.1. Goodness of fit of the fitted total dry weight curves related to Equation 4 in the present study. The SSE, R^2, adjusted R^2, and RMSE represent the sum of squares due to error, coefficient of determination, degree-of-freedom adjusted coefficient of determination, and root mean squared error, respectively.

Treatment	SSE	R^2	Adjusted R^2	RMSE
W200	2.1	0.97	0.96	0.64
W300	2.6	0.97	0.96	0.72
W500	3.9	0.96	0.94	0.99
W700	5.1	0.96	0.95	1.13

Table S3.2. Effects of PPFD on parameters of fruit biomass radiation-use efficiency (FBRUE) component analyses. The results are shown in Fig. 6. Abbreviations within the table are as follows: FBRUE, fruit biomass radiation-use efficiency, g mol^{-1}; RUE, radiation use efficiency, g mol^{-1}; F_{fruits}, fraction of dry mass partitioned to fruits, g g^{-1}; I_{PPFD}, integrated PPFD received by the plant until 82 DAS, mol; W, total dry weight, g; W_{fruit}, fruit dry weight, g; $PPFD_T$, difference between the PPFDs at the top and bottom of the plant (mol m^{-2} s^{-1}); and average PLA, average projected leaf area, m^2. All sampled plants were treated with NPs. All values except FBRUE, RUE, and I_{PPFD} represent the mean ± standard error. Different letters indicate significant differences at $p < 0.05$ ($n = 3-4$) among PPFD treatments with Tukey−Kramer's test.

Treatment	FBRU (g mol^{-1})	RUE (g mol^{-1})	F_{fruits} (g g^{-1})	I_{PPFD} (mol)	W (g)	W_{fruit} (g)	$PPFD_T$ (mol m^{-2} s^{-1})	Average PLA (m^2)
W200	0.59	1.00	0.59 ± 0.06 a	11.0	10.97 ± 0.46 b	6.53 ± 0.70 c	192.2 ± 0.5 d	180.7 ± 11.2 a
W300	0.61	1.04	0.59 ± 0.03 a	10.5	10.90 ± 1.78 b	6.41 ± 1.05 c	297.0 ± 0.6 c	119.5 ± 3.4 b
W500	0.48	0.85	0.57 ± 0.02 a	15.8	13.41 ± 1.10 ab	7.58 ± 0.56 b	495.4 ± 1.13 b	117.2 ± 3.7 b
W700	0.38	0.78	0.49 ± 0.03 b	23.1	18.00 ± 0.89 a	8.86 ± 0.83 a	693.6 ± 1.7 a	117.2 ± 3.6 b

Table S3.3. Effects of fruit pruning on volume, fresh and dry weights, and dry matter content 42 days after anthesis (DAA) in W300, W500, and W700 treatments. OFP and OFT represent one-fruit plants and plants with one fruit per truss. Each value represents the mean ± standard error.

Treatment	PPFD (μmol m^{-2} s^{-1})	Pruning treatment	Fruit age (DAA)	Fruit volume (cm^3)	Single fruit fresh weight (g/fruit)	Single fruit dry weight (g/fruit)
W300	300	OFP	42	8.76 ± 0.95	9.54 ± 0.85	0.98 ± 0.11
		OPT		9.78 ± 0.36	10.59 ± 0.39	1.00 ± 0.04
W500	500	OFP	42	9.14 ± 0.78	9.59 ± 0.86	1.12 ± 0.05
		OPT		7.93 ± 1.38	8.63 ± 1.60	1.00 ± 0.14
W700	700	OFP	42	8.55 ± 0.83	8.64 ± 0.97	1.30 ± 0.13
		OPT		8.72 ± 1.21	8.59 ± 1.37	1.09 ± 0.17

CHAPTER 4.

Effects of light quality on FBRUE in two dwarf tomato cultivars

4.1. Introduction

Tomato plants are divided into two main parts: edible (fruits) and inedible (roots, stems, and leaves) parts. Fruit biomass radiation-use efficacy (FBRUE) can be defined as the ratio of the dry mass of a plant's fruits to the number of photosynthetic photons captured by the plant. It is an important index for the commercial production of tomatoes, indicating the distribution of photoassimilates in fruits. Additionally, FBRUE is a bridge linking photosynthesis and production output.

A quantitative analysis of FBRUE of dwarf tomatoes under different light qualities has not been reported previously. Moreover, the effect of light quality on stomatal conductance in tomatoes varies with the genotype (Ouzounis et al., 2016). Such differences suggest that the effects of red and blue lights on plant biomass production and RUE might be species- and cultivar-specific (Goto, 2003; Wollaeger and Runkle, 2014). Therefore, two dwarf tomato cultivars were used in this study. The objective of this study is to provide an analysis of the effect of light quality on FBRUE of dwarf tomatoes ('Micro-Tom' and 'Rejina') at the reproductive growth stage.

4.2. Materials and methods

4.2.1. Plant materials and growth condition

Two dwarf tomato cultivar, ‘Micro-Tom’ and 'Rejina' (*Lycopersicon esculentum*), were used as the test materials. Tomato seeds were sown in urethane sponge (M-urethane, M Hydroponics Research Co., Ltd., Japan) and kept under dark conditions for three days at 25 ˚C. Seeds germinated on the third day and the plants were cultivated under white LED light lamps (LDL40S-N19/21, Panasonic Corporation., Osaka, Japan) at PPFD 200 μmol m^{-2} s^{-1}. The environmental elements of the cultivation room are described in Table 4.1. All plants were cultivated with the 1/2 OAT house A nutrient (OAT Agrio Co., Ltd., Japan) from ten days after germination. pH and EC of the nutrition solution were set at 6.3 and 1.3 dS m^{-1}, respectively. The nutrition solution was renewed every week.

Table 4.1 Environmental elements in the cultivation room.

Environmental elements	Set value
Photoperiod (h d^{-1})	16
Air temperature (light/dark) (°C)	25/20
Relative humidity (%)	65–70
CO_2 concentration (μmol mol^{-1})	1000

At 24 DAS, seedlings were transplanted under red and blue LED lamps (CIVILIGHT, DPT2RB120Q33 40 type, Showa Denko K.K., Tokyo, Japan; R:B = 9:1) and PPFD above the top of the canopy was set as 300 μmol m^{-2} s^{-1}.

Because the growth rate and anthesis time of the first flower in two cultivars are distinct, the plant density management between two cultivars was different from 35 DAS. The number of days, plant density, used lamps and PPFD on the top of the canopy during growth periods were shown in Table 4.2. The first flowers of half of the plants in Micro-Tom and Rejina bloomed at 36 and 50 DAS, respectively. Finally, when the experiments started, the leaf area (LA) / projected leaf area (PLA) values of Micro-Tom at 36 DAS and of Rejina at 50 DAS were modulated at 1.5 and 1.6, respectively (Figure 4.1).

Table 4.2. The number of days, plant density, used lamps and PPFD on the top of the canopy during different growth periods in two cultivars.

Cultivar	Growth period (DAS)	The number of days	Plant density (plant/m^2)	PPFD (μmol m^{-2}s^{-1})	Lamps
Micro-Tom	0–23	23	800	200	White LED lamps[x]
	24–35	11	476.2	300	Red and Blue LED lamps[y]
	36–82	47	238.1	300	Depend on the treatment
Rejina	0–23	23	800	200	White LED lamps[x]
	24–43	19	261	300	Red and Blue LED lamps[y]
	44–49	5	55.9	300	Red and Blue LED lamps[y]
	50–100	50	37.3	300	Depend on the treatment

[x] White LED lamps (LDL40S-N19/21, Panasonic Corporation., Osaka, Japan).

[y] Red and blue LED lamps (CIVILIGHT, DPT2RB120Q33 40 type, Showa Denko K.K., Tokyo, Japan; R:B = 9:1).

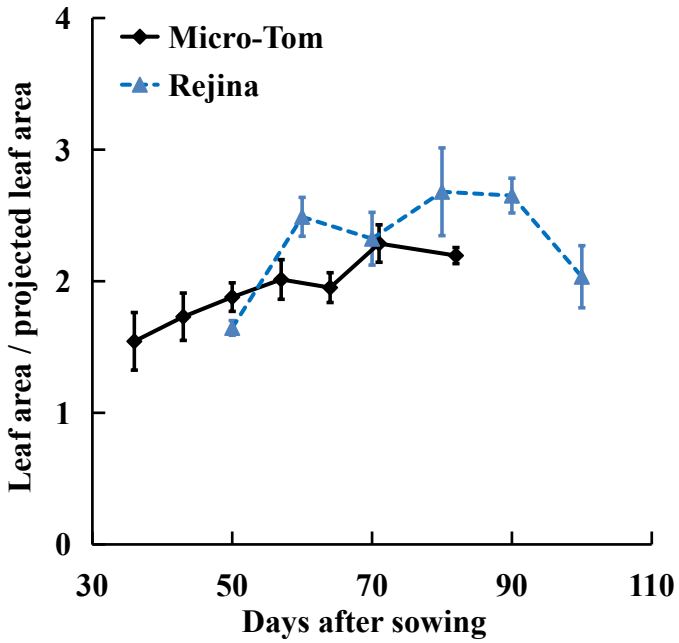

Figure 4.1. Leaf area / projected leaf area changes of two dwarf tomato cultivars over time. Each value represents the average of 12 values (n = 12). Error bars represent ± standard error.

After 36 DAS in Micro-Tom and 50 DAS in Rejina, plants was placed in four treatments with different light qualities: red light (R), white light (W) and a mixture of red and blue lights, R3B1 (R:B = 3:1) and R9B1 (R:B = 9:1). The PPFD above the top

of all canopy was set as 300 μmol m^{-2} s^{-1}. The other environmental conditions were the same as those shown in Table 4.1. pH and EC of the nutrition solution were set at 6.0 and 2.1 dS m^{-1} during the reproductive growth stage, respectively. For all plants, side shoots and axillary buds were pruned when they were visible. Final harvests were conducted when the half of fruits turned red at 82 DAS in Micro-Tom and at 100 DAS in Rejina, respectively. The spectral photon flux distributions of the LED lamps were measured using a spectroradiometer (USR-45DA, USHIO Inc., Tokyo, Japan), as shown in Figure 4.2. The fractions of blue, green, and red wavelengths, as well as red/blue ratio, were calculated (Table 4.3).

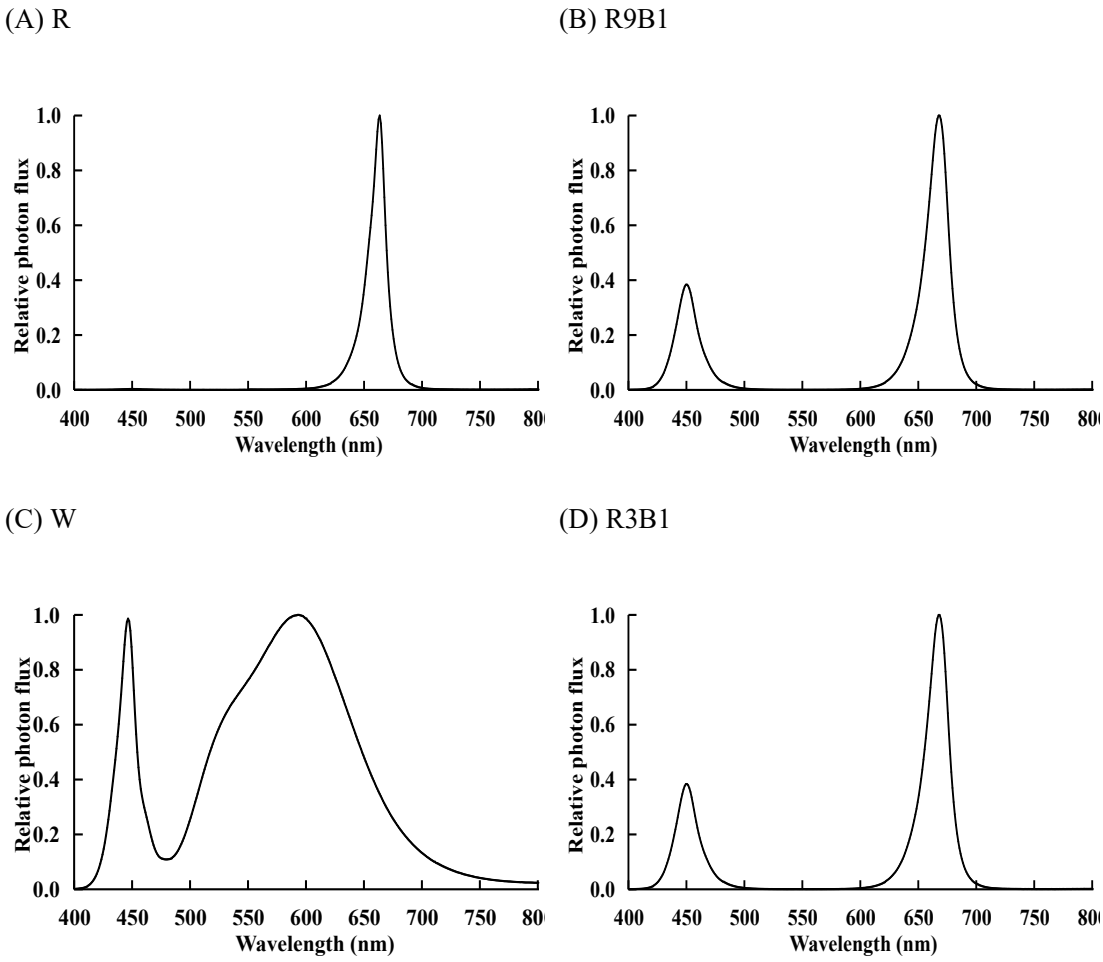

Figure 4.2. Spectral photon flux distributions of red LED lamp (A), red and blue LED lamps in R9B1 (B), white LED lamp (C) as well as red and blue LED lamps in R3B1 (D). R3B1 and R9B1 represent photon flux ratios (red to blue light) of 3:1 and 9:1, respectively. The peak wavelengths of the white lamp were 446 nm and 592 nm. The peak wavelengths of red and blue light were 667 and 450 nm, respectively. The maximum value of photon flux was converted to 1.0.

Table 4.3. Spectral data for LED lamps at the wavelength of 400–700 nm. '%' represents the ratios of blue, green, red, and far-red photon fluxes as a percentage of photon flux density. R/B ratio represents the photon flux ratio of red light to blue light. 'R' respects red LED lamps. 'W' represents white LED lamps. R3B1 and R9B1 represent red-blue LED lamps with photon flux ratios of 3:1 and 9:1, respectively, of red to blue light. The phytochrome photostationary state (PSS) is calculated using spectral composition and intensity of light received by plants (Sager and Smith, 1988; Stutte, 2009).

	R	**R9B1**	**W**	**R3B1**
% Blue (400–499 nm)	0.2	9.9	17.1	24.5
% Green (500–599 nm)	0.5	0.4	46.7	0.4
% Red (600–699nm)	98.3	89.0	32.9	74.7
% Far-red (700–800 nm)	1.0	0.7	3.3	0.4
R/B ratio	-	9.0	1.9	3.0
PSS	0.88	0.88	0.85	0.87

4.2.2. Growth measurement

Three or four plants in each treatment were destructively sampled for biomass analysis and leaf area measurement at 36, 43, 50, 57, 64, 71 and 82 DAS in Micro-Tom and at 50, 60, 70, 80, 90 and 100 DAS in Rejina, respectively. Plant organs were dried for 72 h at 80 ˚C in a convection oven. The plant height was measured from the main stem base to the top of the plant with a ruler. Both Micro-Tom and Rejina are determinate tomatoes and there is no new leaf on the main stem after the first fruit truss. LA was measured with a leaf area meter (LI-3000C, Li-Cor Inc., Lincoln, NE, USA). Specific leaf area (SLA, $cm^2\ g^{-1}$) was calculated by dividing LA (cm^2) by the leaf dry weight (g). The number of fruits was recorded too. All growth parameters at 82 DAS in Micro-Tom and at 100 DAS in Rejina were measured in two replicates, respectively.

4.2.3. Fruit quality

Brix and acidity of 6−9 ripe tomatoes from three or four plants in every treatment were measured with a pocket Brix-Acidity Meter (PAL-BX|ACID3; Atago Co. Ltd.) as

parameters of fruit quality at 82 DAS in Micro-Tom and 100 DAS in Rejina, respectively.

4.2.4. Leaf optical properties

A spectrophotometer (V-750, JASCO Corporation, Tokyo, Japan) was used to measure the reflection and transmission spectra of the first leaf from the top of the main stem (fully expanded and unshaded leaf) at 50, 71 and 82 DAS in Micro-Tom and at 50, 60, 70 and 80 DAS in Rejina with an integrating sphere unit (ISV-922, JASCO Corporation, Tokyo, Japan). The measured light spectrum ranged from 400 nm to 700 nm. Three plants were sampled per treatment. For each wavelength, the absorptance was calculated as 100% minus reflectance and transmittance.

4.2.5. Pn

The Pn was determined for the the first leaf from the top of the main stem (fully expanded and unshaded leaf) of three randomly selected plants in each treatment at 53, 67 and 81 DAS using a portable photosynthesis measurement system (LI-6400XT, LI-COR Inc., Lincoln, NE, USA), equipped with a transparent cuvette under the following environmental conditions: 25 ± 1 °C leaf temperature, 65–70% relative humidity, and 1000 μmol mol^{-1} CO_2 concentration. The leaves were clamped into the cuvette until the Pn and stomatal conductance were stable at every measurement. The flow rate of air through the system was set to 500 μmol s^{-1}.

4.2.6. Chlorophyll concentration

Chlorophyll pigment was extracted from the first leaf from the top of the main stem (fully expanded and unshaded leaf) with N,N-dimethylformamide at 50, 71 and 82 DAS in Micro-Tom and at 50, 70, 80 and 100 DAS in Rejina, respectively, according to the protocol described by Porra et al. (1989). For chlorophyll concentration analysis, three or four leaves from three or four plants in each treatment were sampled. The chlorophyll concentration was determined on a dry weight basis by measuring the

absorbance of the leaf extracts at 663.8, 646.8, and 750.0 nm using an ultraviolet-visible spectrophotometer (V-750, JASCO Corporation, Tokyo, Japan).

4.2.7. RUE

RUE (g mol^{-1}) was defined as the proportion of the accumulated dry mass (ΔW, g) to the integrated PPFD received by the plant during a given period (ΔI_{PPFD}, mol). RUE was considered as a constant during the whole reproductive growth stage in this study. Therefore, the slope of the fitted regression line to illustrate the relationship between ΔW and ΔI_{PPFD} was the value of RUE.

To maintain 300 μmol m^{-2} s^{-1} PPFD at the top of the canopies, a quantum sensor (LI-190, Lincoln, NE, USA) and GaAsp photodiodes (G1118, Hamamatsu Photonics K. K., Shizuoka, Japan) were used. The quantum sensor was also used to measure the PPFD of 29–51 evenly distributed points at every 3 to 5 days at the bottom of the canopy. The intercepted PPFD of the canopy was equal to the difference between the average PPFD at the top and bottom. The intercepted PPFD proportion was calculated by dividing the intercepted PPFD by the average PPFD at the canopy top. The intercepted PPFD proportion and PLA between two consecutive measured values increased linearly, and those on unmeasured days were estimated based on the measured values.

Free imaging software (LIA 32 ver. 0.378, Yamamoto) was used to determine the projected leaf area (PLA) from photos of the canopy on the same days that PPFD measurements were taken. Each parameter used in the calculation of RUE was measured in three replicates.

4.2.8. FBRUE

FBRUE is the product of RUE (g mol^{-1}) and the fraction of dry mass partitioned into fruits (F_{fruits}, g g^{-1}) on a given day. F_{fruits} (g g^{-1}) is defined as the ratio of the dry mass of tomato fruits to the total dry mass of the plant.

4.2.9. The power of lamps

Power consumption of LED lamps in each treatment was measured by a portable power monitor (Omron ZN-CTX21, OMRON Corporation, Kyoto, Japan).

4.2.10. Statistical analysis

One-way analysis of variance (ANOVA) was performed using SPSS for Windows (Version 24.0; SPSS Inc., Chicago, IL, USA) to analyze the data in a cultivar. A Tukey-Kramer test at $p < 0.05$ was used to compare the mean values of measured data to investigate significant differences among treatments in the same cultivar. Measurements about FBRUE in each treatment were repeated three times.

4.3. Results and discussion

4.3.1. Growth characteristics

Light quality significantly affected the SLA in the two cultivars (Table 4.4). In addition, light quality also had significant effects on total dry weight ratio in Micro-Tom and plant height in Rejina, respectively. SLAs of the two cultivars in R without blue light were the highest and significantly higher than those in R3B1 which had the highest blue light ratio. Rejina plants grown under monochromatic red light showed typical shade-avoidance characteristics, namely decreased leaf thickness and increased stem elongation and leaf area. In general, blue light reduces cell expansion and thus inhibits leaf growth and stem elongation (Cosgrove, 1981). Matsuo et al. (2019) reported that the light intensity of blue LED negatively correlated with the stem length because blue light increased the transcript level of *SlGA2ox7* and controlled gibberellin (GA) inactivation which may affect stem elongation. However, light quality hardly affected the plant height of Micro-Tom. Martí et al., (2006) found that Micro-Tom is not a GA-deficient cultivar. GAs and brassinosteroids act synergistically in Micro-Tom, and the response to GA depends on brassinosteroids. Therefore, the light quality might not change GA or brassinosteroids concentrations sufficiently to cause significant changes in plant height of dwarf tomatoes. Moreover, until 36 DAS when the first flower in Micro-Tom bloomed, Micro-Tom plant was higher and larger than that of Rejina (Figure S4.1 (A)). However, Rejina plant was higher and larger than that of Micro-Tom plant at 50 DAS (Figure S4.1 (B)).

Table 4.4. Effect of light quality on the growth of 'Micro-Tom' 82 days after sowing (DAS) and of 'Rejina' 100 DAS. DW is dry weight (g). Each value represents the mean ± standard error. Different letters in a column in a cultivar indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 6−8). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

Cultivar	Initial value or treatment	Plant height (cm)	Total fresh weight (g)	Total dry weight (g)	Total dry matter ratio (%)	Specific leaf area ($cm^2\ g^{-1}$ DW)
Micro-Tom	Initial value at 36 DAS	10.3 ± 0.4	10.2 ± 0.7	0.9 ± 0.1	8.9 ± 0.3	288.5 ± 13.7
	R	12.7 ± 0.7	118.8 ± 12.7	10.4 ± 1.6	8.6 ± 0.5 b	157.2 ± 17.4 a
	R9B1	12.1 ± 0.3	115.0 ± 9.8	10.9 ± 0.9	9.5 ± 0.4 ab	133.0 ± 8.5 ab
	W	11.3 ± 0.3	104.6 ± 17.4	10.9 ± 1.8	10.5 ± 0.1 a	115.7 ± 4.8 ab
	R3B1	13.2 ± 0.2	133.9 ± 5.8	13.1 ± 0.5	9.8 ± 0.2 ab	109.0 ± 1.6 b
Rejina	Initial value at 50 DAS	13.7 ± 0.4	69.4 ± 2.0	6.5 ± 0.2	9.3 ± 0.2	186.9 ± 11.9
	R	21.7 ± 1.7 a	382.2 ± 67.0	31.2 ± 4.5	8.3 ± 0.6	136.4 ± 6.8 a
	R9B1	18.5 ± 0.8 ab	416.8 ± 85.3	34.7 ± 5.7	8.5 ± 0.3	113.6 ± 1.3 b
	W	16.5 ± 0.3 b	435.7 ± 57.7	35.4 ± 5.1	8.1 ± 0.1	102.0 ± 3.4 b
	R3B1	19.0 ± 0.8 ab	452.4 ± 91.1	37.0 ± 6.0	8.4 ± 0.4	110.3 ± 4.2 b

There were no significant differences in total dry weights in two cultivars (Table 4.4). This result was different with the finding that a high percentage of blue light can inhibit biomass production in tomato seedlings (cv. Early girl) at 200 and 500 μmol m^{-2} s^{-1} PPFDs (Snowden et al., 2016). However, in the same paper, there were no significant differences in dry mass among different light qualities in cucumber at 200 μmol m^{-2} s^{-1} PPFD, in radish, soybean, lettuce (cv. Waldmann's Green), and wheat at 200 and 500 μmol m^{-2} s^{-1} PPFDs. The dry mass of lettuce plants 'Gentilina' (Lactuca sativa cv. Rebelina, Gautier, Eyragues, France) decreased and then increased with an increase of percentage of blue light at 215 μmol m^{-2} s^{-1} PPFD (Pennisi et al., 2019). The reason might be that the effects of red:blue light ratio (R/B ratio) on stomatal conductance and photosynthetic rate in tomatoes are highly cultivar-specific (Ouzounis et al., 2016).

4.3.2. Leaf optical properties

Photosynthetically active radiation (PAR) was most reflected and least absorbed by the top leaves in R in the two cultivars (Tables 4.5 and 4.6). In addition, the transmittance of Rejina leaves in R was significantly higher than those in other treatments (Table 4.6). The SLA in R was significantly higher than those in R3B1 in the two cultivars (Table 4.4). Leaf anatomy may directly influence light capture by its leaf thickness as well as by the differentiation of palisade and spongy mesophyll. An earlier report showed that leaf thickness increased when red light was supplemented with blue light (Schuerger et al., 1997). There were no significant differences in leaf optical properties among all treatments at 50 and 71 DAS in Micro-Tom and 50, 70 and 80 DAS in Rejina (data not shown). Therefore, the effects of light quality on leaf optical properties appeared significantly in the late period of the reproductive growth stage.

Table 4.5. Effects of light quality on the reflectance and absorptance of leaves in 'Micro-Tom' at the blue, green and red wavelengths 82 DAS ['Micro-Tom']. The range of measured light spectrum was 400–700 nm. Each value represents the mean ± standard error. Different letters in a column in a cultivar indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3−4). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

Treatment	Reflectance (%)			Absorptance (%)		
	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)
R	6.8 ± 0.0	9.3 ± 0.0 a	7.2 ± 0.0 a	93.0 ± 0.1	86.1 ± 1.2 b	90.9 ± 0.6 b
R9B1	4.9 ± 0.1	6.3 ± 0.0 ab	5.0 ± 0.1 ab	95.0 ± 0.1	90.8 ± 0.8 a	94.0 ± 0.3 a
W	3.7 ± 1.8	5.2 ± 1.4 b	3.8 ± 1.4 b	96.1 ± 1.7	89.4 ± 0.4 a	94.0 ± 0.9 a
R3B1	5.1 ± 0.5	6.1 ± 0.4 ab	4.8 ± 0.0 ab	94.8 ± 0.5	91.8 ± 0.7 a	93.1 ± 0.0 a

Table 4.6. Effects of light quality on the reflectance, transmittance and absorptance of leaves in 'Rejina' at the blue, green and red wavelengths 100 DAS ['Rejina']. The range of measured light spectrum was 400–700 nm. Each value represents the mean ± standard error. Different letters in a column in a cultivar indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3−4). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

Treatment	Reflectance (%)			Transmittance (%)			Absorptance (%)		
	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)	400–499 nm (Blue)	500–599 nm (Green)	600–700 nm (Red)
R	5.6 ± 0.1	8.9 ± 0.4 a	7.7 ± 0.5 a	0.5 ± 0.1 a	5.7 ± 0.7 a	3.3 ± 0.4 a	94.1 ± 0.1 b	85.7 ± 0.6 b	88.7 ± 0.2 b
R9B1	5.5 ± 0.0	6.5 ± 0.1 b	6.2 ± 0.1 ab	0.1 ± 0.0 b	1.8 ± 0.4 b	0.9 ± 0.2 b	94.5 ± 0.0 ab	91.7 ± 0.5 a	92.9 ± 0.3 a
W	5.0 ± 0.3	5.9 ± 0.1 b	5.3 ± 0.5 b	0.1 ± 0.0 b	2.5 ± 0.6 b	1.3 ± 0.2 b	94.9 ± 0.3 ab	91.6 ± 0.6 a	93.4 ± 0.5 a
R3B1	4.7 ± 0.3	5.8 ± 0.5 b	5.1 ± 0.0 b	0.1 ± 0.0 b	1.7 ± 0.1 b	1.6 ± 0.0 b	95.3 ± 0.3 a	92.5 ± 0.4 a	93.3 ± 0.0 a

4.3.3. Pn and chlorophyll concentration

The values of Pn in R at 53, 67 and 82 DAS were the lowest among all treatments in Micro-Tom (Figure 4.3). At 67 DAS, the Pn in R was significantly lower than others in Micro-Tom. Similar to Micro-Tom, the values of Pn in Rejina under red light were significantly lower than those in W at 53 and 67 DAS (Figure 4.4). A low photosynthetic rate in plants grown under red light alone has been shown for several crop plants. Matsuda et al. (2004) found a lower photosynthetic rate for rice grown under red LEDs alone than for plants grown under a mixture of red and blue LEDs. Similar results were found for wheat (Goins et al., 1997), which had a lower photosynthesis and dry mass accumulation when grown under red alone compared with growth under white fluorescent tubes or under red light supplemented with blue. While Yorio et al. (2001) reported a lower dry mass accumulation in radish, spinach and lettuce grown under red LEDs alone than under white fluorescent tubes or red supplemented with blue, only radish developed a lower photosynthetic rate when grown under red LEDs.

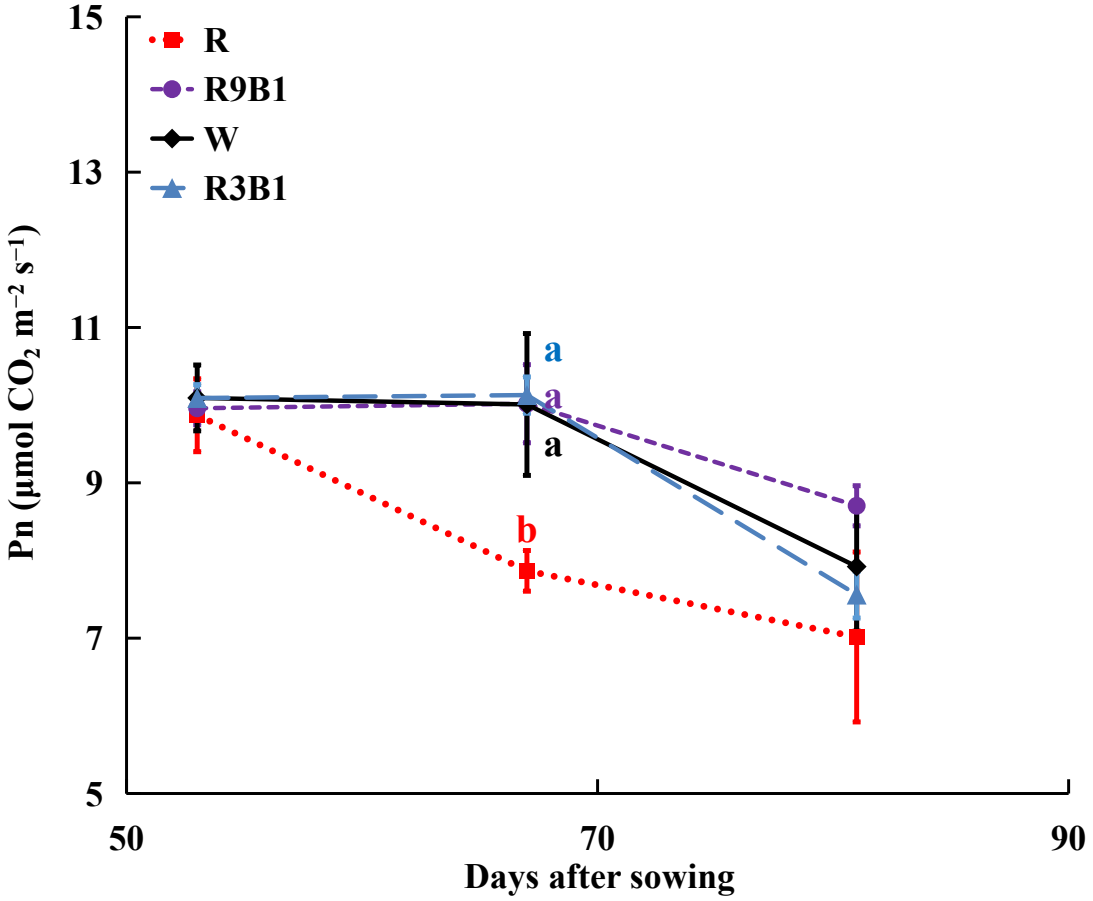

Figure 4.3. Effect of light quality on net photosynthetic rate (Pn) in 'Micro-Tom' 53, 67 and 81 DAS ['Micro-Tom']. Solid point represents the average Pn of three or four plants in each treatment. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3−4). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

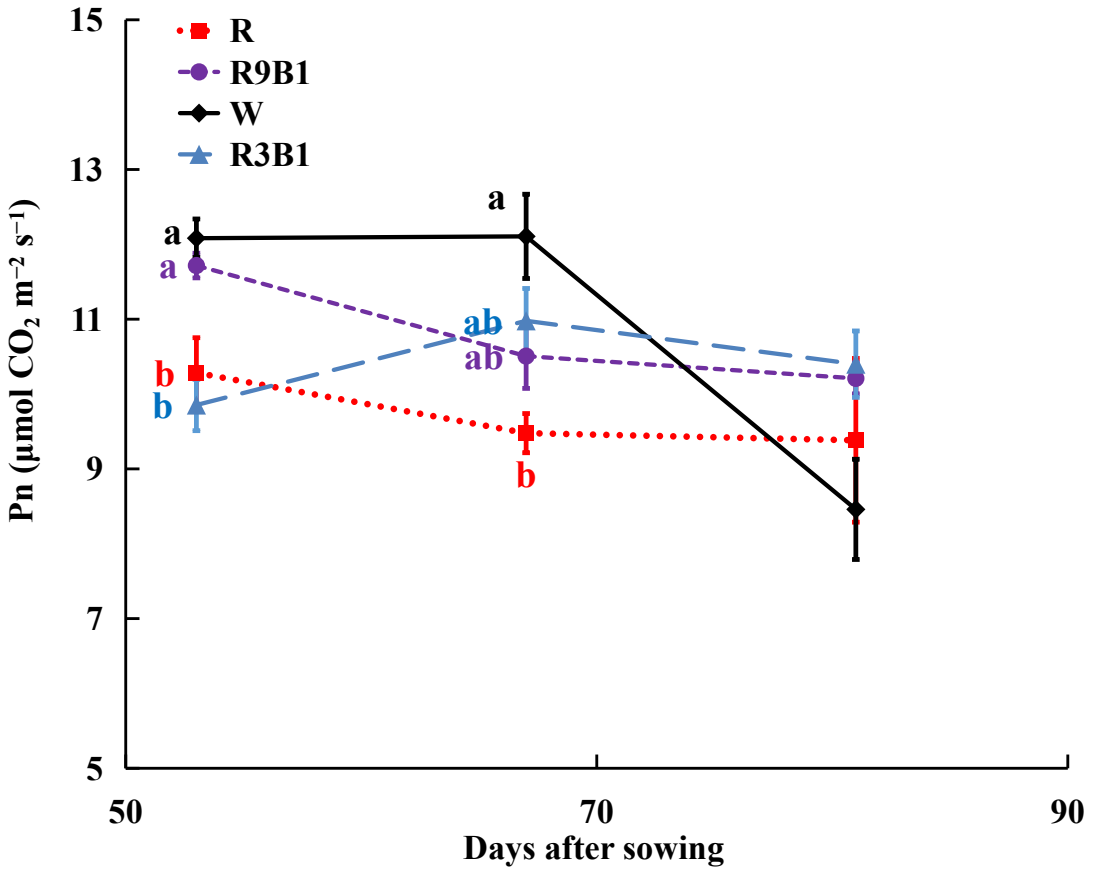

Figure 4.4. Effect of light quality on net photosynthetic rate (Pn) in 'Rejina' 53, 67 and 81 DAS ['Rejina']. Solid point represents the average Pn of three or four plants in each treatment. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3−4). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

The deficiency of blue in R might be the reason why the Pn in R was the lowest. An increasing proportion of blue light was associated with a decrease in SLA, and an increase in chlorophyll concentration, and nitrogen content per unit leaf area in cucumber leaves (Hogewoning et al., 2010). In the case of Micro-Tom and Rejina, higher proportion of blue light indeed decreased the SLA (Table 4.4) but did not increase chlorophyll concentration (Figure S4.2). In addition, blue light can improve stomatal density and conductivity (Chartzoulakis et al., 2000) which might be the reason why the values of Pn in R9B1 and R3B1 were significantly higher than that in

R at 67 DAS in Micro-Tom (Figure 4.3). In addition, the values of Pn in the two cultivars decreased with time. This might be due to the leaf senescence (Quirino et al., 2000).

The Pn in W was high until 67 DAS in the two cultivars (Figures 4.3 and 4.4). In this study, the white LED light has 3.3% far-red photons (Table 4.3) which might increase Pn. Zhen and van Iersel (2017) found that adding supplemental far-red photons from LEDs (peak at 735 nm) to red+blue or white LED light synergistically increased the quantum yield of PSII and leaf photosynthetic rate over a wide range of light intensities (also see Murakami et al., 2018). The enhancement was slightly larger under the red/blue background light than under a warm white LED, probably because the warm white LED light already had 4% far-red photons.

Light quality significantly affected the concentration of chlorophyll a+b in the two cultivars (Figures 4.5 and 4.6). The chlorophyll concentration of leaves in Micro-Tom in W was significantly lower than those in other treatments at 71 DAS (Figure 4.5). At 82 DAS, it in Micro-Tom in R was significantly higher than those in W and R3B1. Similar to Micro-Tom, the chlorophyll concentration of leaves in Rejina in W was significantly lower than those in other treatments at 80 DAS (Figure 4.6) and it in R was significantly higher than that in W at 100 DAS. Monochromatic red light might increase the chlorophyll a and b. This result was contrary to some studies. Matsuda et al. (2007) reported that the chlorophyll content per unit leaf area in spinach increased first and then decreased with the increase of blue light PFD. Wang et al. (2009) reported that blue light enhanced the expression of different enzymes such as MgCH, GluTR, and FeCH which regulate the synthesis of chlorophyll in cucumber. Red light is less conducive for the chlorophyll biosynthesis, because of its reduction of the tetrapyrrole precursor 5-aminolevulinic acid (Sood et al., 2005; Fan et al., 2013). However, our results were same with *F. benjamina* study (Zheng and Van Labeke, 2017). In addition, Hogewoning et al. (2007) also reported an increase of blue light ratio from 0 to 50% increased the chlorophyll content per unit leaf area (g m^{-2}) but decreased the chlorophyll concentration (g g^{-1}) on a leaf dry weight basis in cucumber which was

similar to our results. This differential response might be due to species effect.

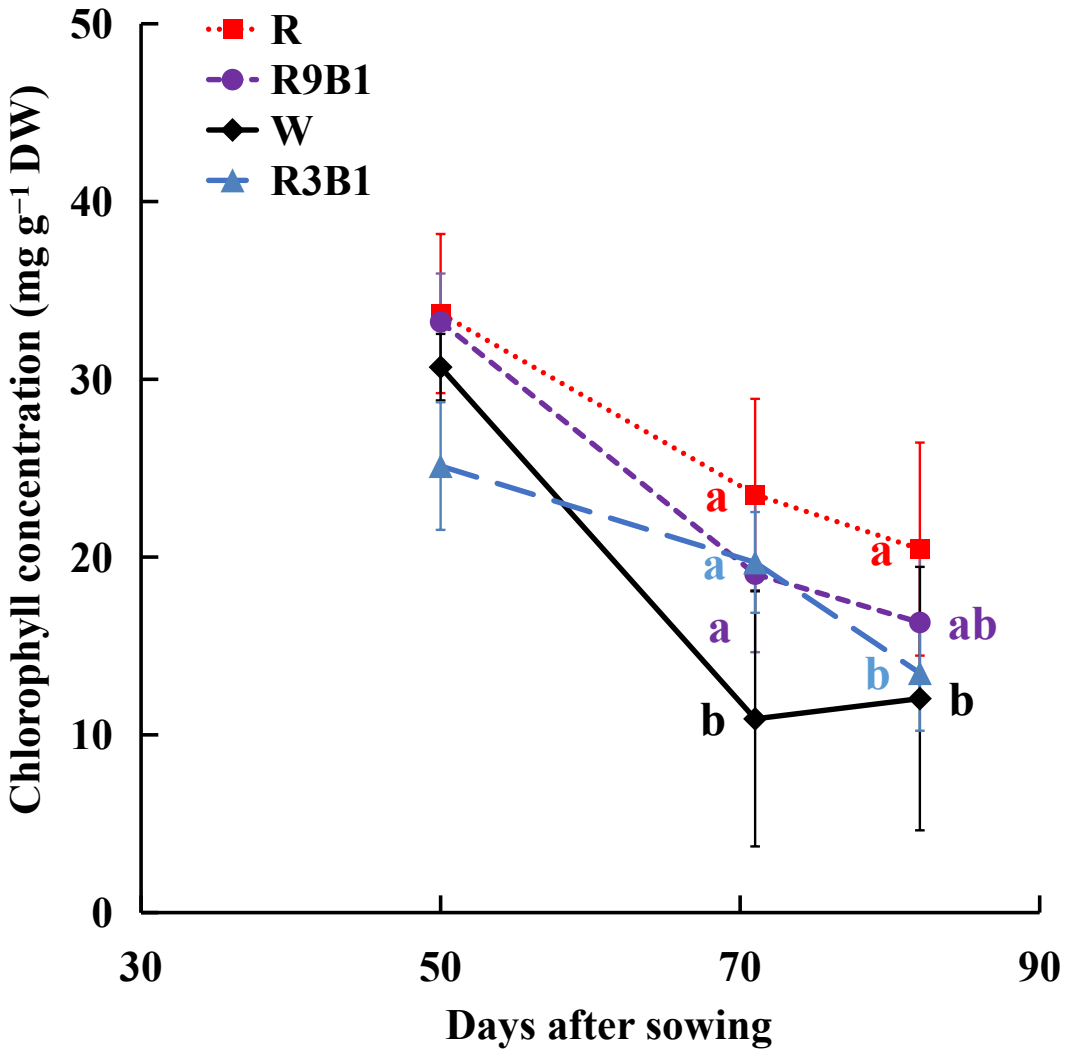

Figure 4.5. Effect of light quality on chlorophyll concentration of leaves in 'Micro-Tom' 50, 71 and 82 DAS ['Micro-Tom']. DW (g) is dry weight. Solid point represents the average value of three plants in each treatment. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

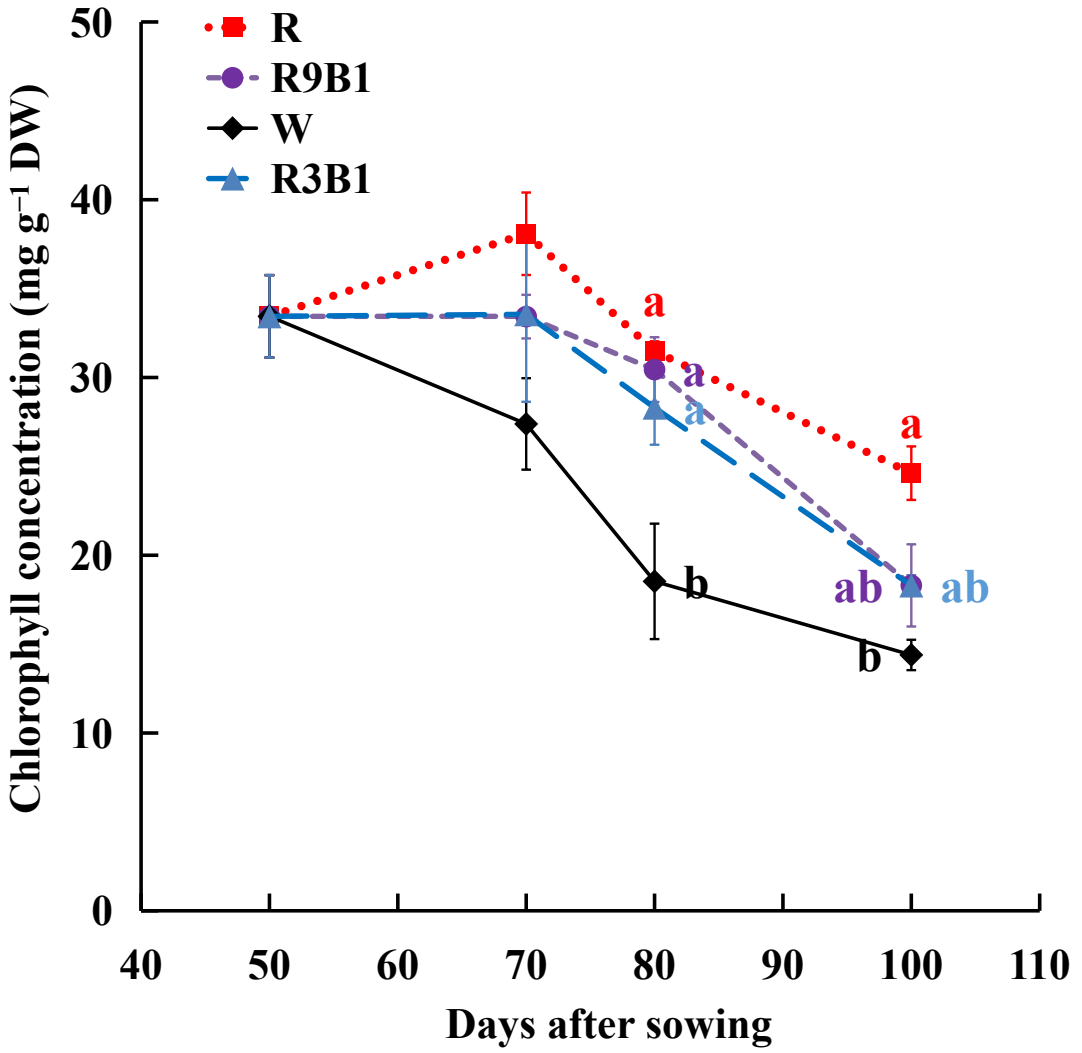

Figure 4.6. Effect of light quality on chlorophyll concentration of leaves in 'Rejina' 50, 70, 80 and 100 DAS ['Rejina']. DW (g) is dry weight. Solid point represents the average value of three plants in each treatment. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

4.3.4. RUE

The values of RUE in W and R3B1 were significantly higher than those in R and R9B1 in Micro-Tom (Figure 4.7). Similarly, the RUE value in W was the highest and in R was the lowest among all treatments in Rejina (Figure 4.8). The blue light

proportions of R, R9B1, W and R3B1 were 0, 10%, 17% and 25%, respectively (Table 4.3). RUE increased with an increase of the blue light proportion from 0 to 17% and decreased with the increase until 25% in the two cultivars (Figures 4.7 and 4.8).

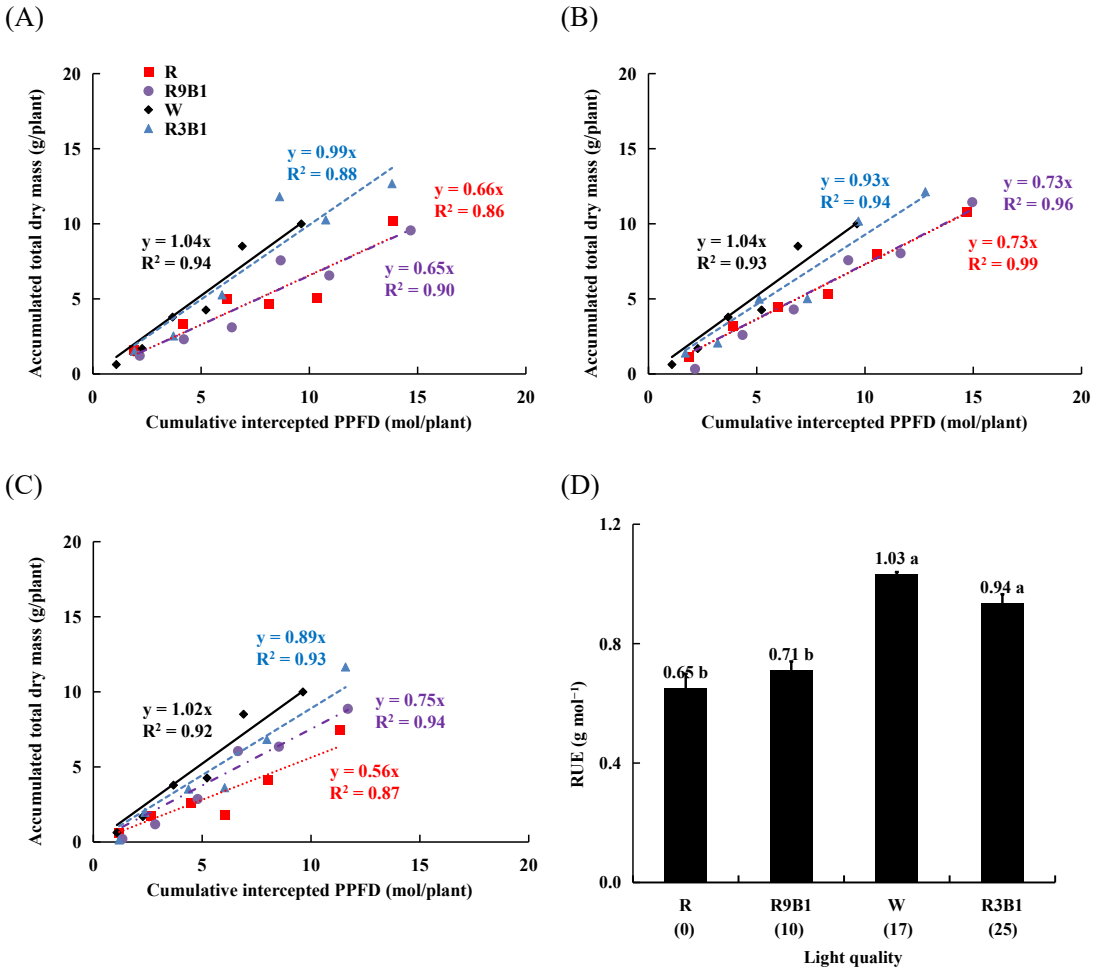

Figure 4.7. Relationships between accumulated dry weights (ΔW) and cumulative intercepted PPFDs (ΔI_{PPFD}) per plant and RUE in 'Micro-Tom' under different light qualities during the reproductive growth stage ['Micro-Tom']. (A), (B), (C) were the results of three repetitions, respectively. The slope of the fitted linear relationship is the RUE at the reproductive growth stage. The RUE in (D) was calculated using the data in (A−C). The numbers in the brackets of x-axis are the ratios of blue photon fluxes as a percentage of photon flux density (%) in D. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

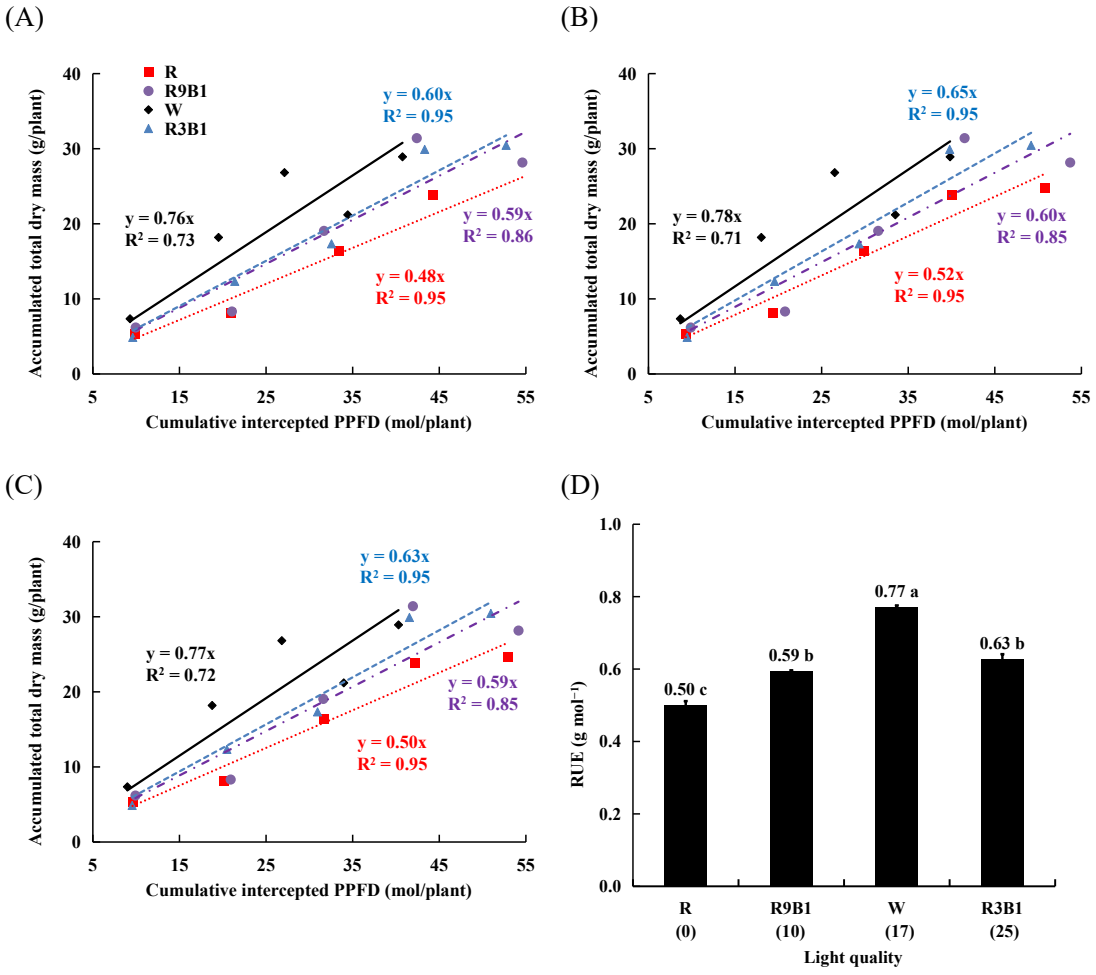

Figure 4.8. Relationships between accumulated dry weights (ΔW) and cumulative intercepted PPFDs (ΔI_{PPFD}) per plant and RUE in 'Rejina' under different light qualities during the reproductive growth stage ['Rejina']. (A), (B), (C) were the results of three repetitions, respectively. The slope of the fitted linear relationship is the RUE at the reproductive growth stage. The RUE in (D) was calculated using the data in (A−C). The numbers in the brackets of x-axis are the ratios of blue photon fluxes as a percentage of photon flux density (%) in D. Error bars represent ± standard error. Different letters indicate significant differences among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

There might be two reasons why RUE in W was the highest. Firstly, the change trend of RUE under different light qualities was associated with Pn changes in the two

cultivars (Figures 3 and 4). The highest Pn led to the highest RUE in W. There was a far-red promotion (Zhen and van Iersel, 2017; Ji et al., 2020) in Pn if the light contains far-red radiation. The white LED lamp in this study had 3.3% far-red radiation. Secondly, the white LED lamp in this study had 46.7 % green light while while other light qualities had less than 1% green light. The green light can penetrate further into the leaf than red or blue light, more green light absorbed by the leaves in the lower canopy (Terashima et al., 2009). It is also known that green light, once absorbed by the leaves, drives photosynthesis with high efficiency (Björkmann, 1968; McCree, 1972). More green light in W might enhance the canopy RUE by improving the uniformity of light distribution throughout the canopy.

It is well known that at least a low percentage of blue light is necessary in supplementing red light for optimal plant growth (Hoenecke et al., 1992; Cope and Bugbee, 2013). However, there was no blue light in R. Not only Pn (Figures 4.3 and 4.4) but also absorptance of leaves in R (Tables 4.5 and 4.6) were significantly lower than other treatments. That might be the reason why the RUE in R was the lowest in the two cultivars (Figures 4.3 and 4.4).

Although the two cultivars could not be compared statistically due to the inconsistency of plant density and light environment, it was interesting that the RUE of Micro-Tom was higher than Rejina under all light qualities even the Pn of Rejina was higher than Micro-Tom. There might be two reasons. Firstly, the respiration rate of Rejina was higher than than of Micro-Tom (Figure S4.3). More dry mass was consumed during the dark period. Secondly, there were about 10 true leaves in Rejina and 6 true leaves in Micro-Tom. The fifth true leaf from the bottom in Rejina and the sixth true leaf in Micro-tom was expanded at 36 DAS (Figure S4.1 (A)). The age of the top leaf in Rejina was younger than that in Micro-Tom at the same DAS. In addition, until harvest, the age of the bottom leaf in Micro-Tom was younger than that in Rejina. In addition, the top leaves (2–3 leaves) in Rejina occupied 20–30% and in Micro-Tom occupied 30–50%. Therefore, the Pn (μmol m^{-2} s^{-1}) of the whole canopy in Rejina

might be less than that in Micro-Tom. In the future, the Pn of the whole canopy should be measured and used for the study about the RUE of the canopy.

4.3.5. Dry mass partitioning to fruits and FBRUE

In Micro-Tom, the F_{fruits} increased from 36 DAS to 71 DAS in all treatments and kept stable until 82 DAS (Figure 4.9). There was no significant difference in F_{fruits} at 82 DAS among treatments.

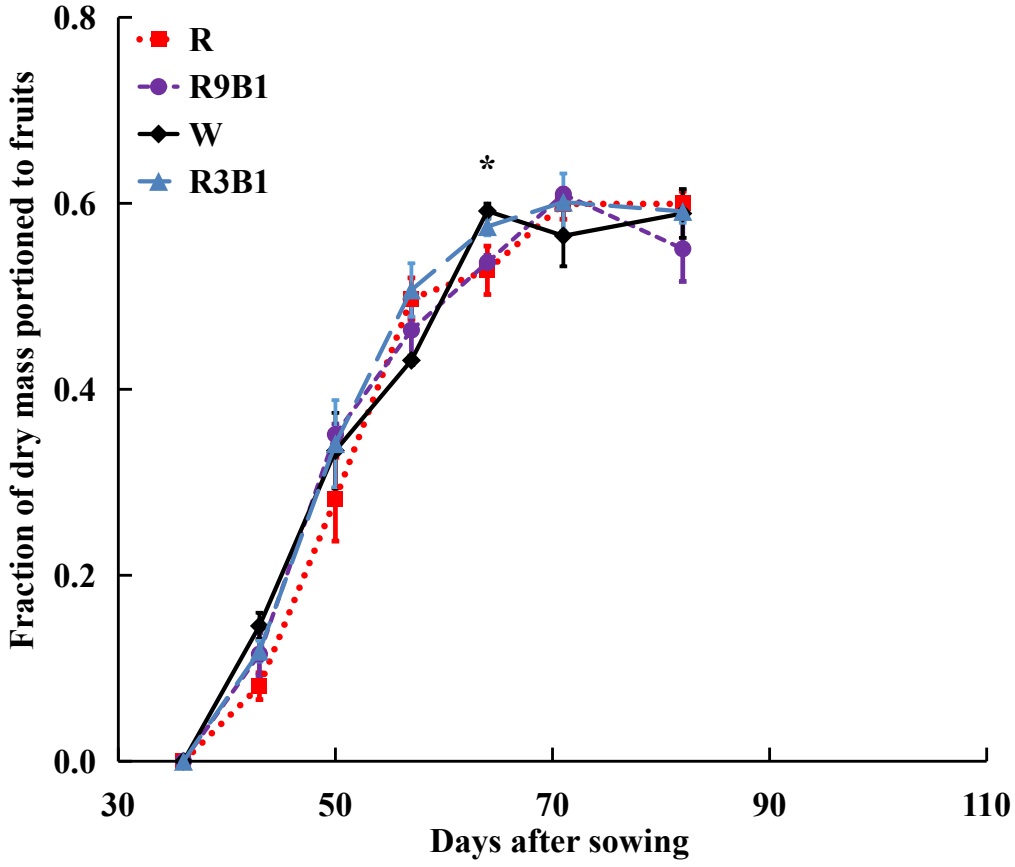

Figure 4.9. Effect of light quality on the fraction of dry mass portioned to fruits (F_{fruits}) over time in 'Micro-Tom' ['Micro-Tom']. Error bars represent ± standard error. * indicates significant difference among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3−6). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

In Rejina, the F_{fruits} increased from 50 DAS to 90 DAS in all treatments and decreased until 100 DAS expect W (Figure 4.10). The F_{fruits} values in W and R3B1 were significantly higher than that in R9B1 at 90 DAS. Moreover, the F_{fruits} in W was significantly higher than those in other treatments at 100 DAS. More red-light ratio and low blue-light led to higher dry mass partitioning to leaves in tomatoes under red and blue LED light (Liang et al., 2021). This result also agrees with those of Thwe et al. (2020), who observed a higher shoot-root ratio under high red-to-blue ratio light in tomatoes (cv. Sida). In the present study, the dry mass partitioning to leaves in R and R9B1 was higher than those in W and R3B1 in Micro-Tom at 64 DAS (data no shown). In addition, far-red light promotes fruit growth by increasing dry mass partitioning to fruits (Ji et al., 2019). That might be the reason why F_{fruits} was the highest at 90 and 100 DAS in Rejina (Figure 4.10).

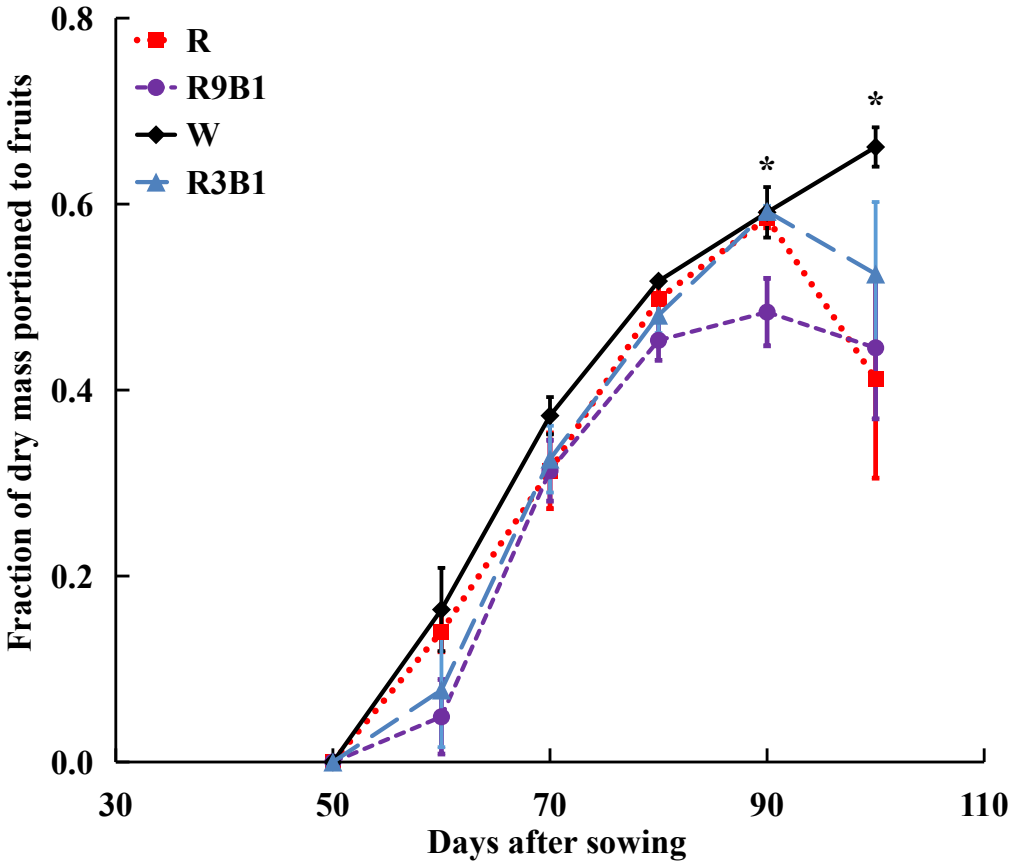

Figure 4.10. Effect of light quality on the fraction of dry mass portioned to fruits (F_{fruits}) over time in 'Rejina' ['Rejina']. Error bars represent ± standard error. * indicates significant difference among the treatments based on Tukey−Kramer's test at $p < 0.05$ (n = 3−6). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

In Micro-Tom, FBRUE was significantly affected by light quality at 43, 57, 64, 71 and 82 DAS (Figure 4.11). The FBRUE values in W and R3B1 were significantly higher than those in R and R9B1 from 64 DAS.

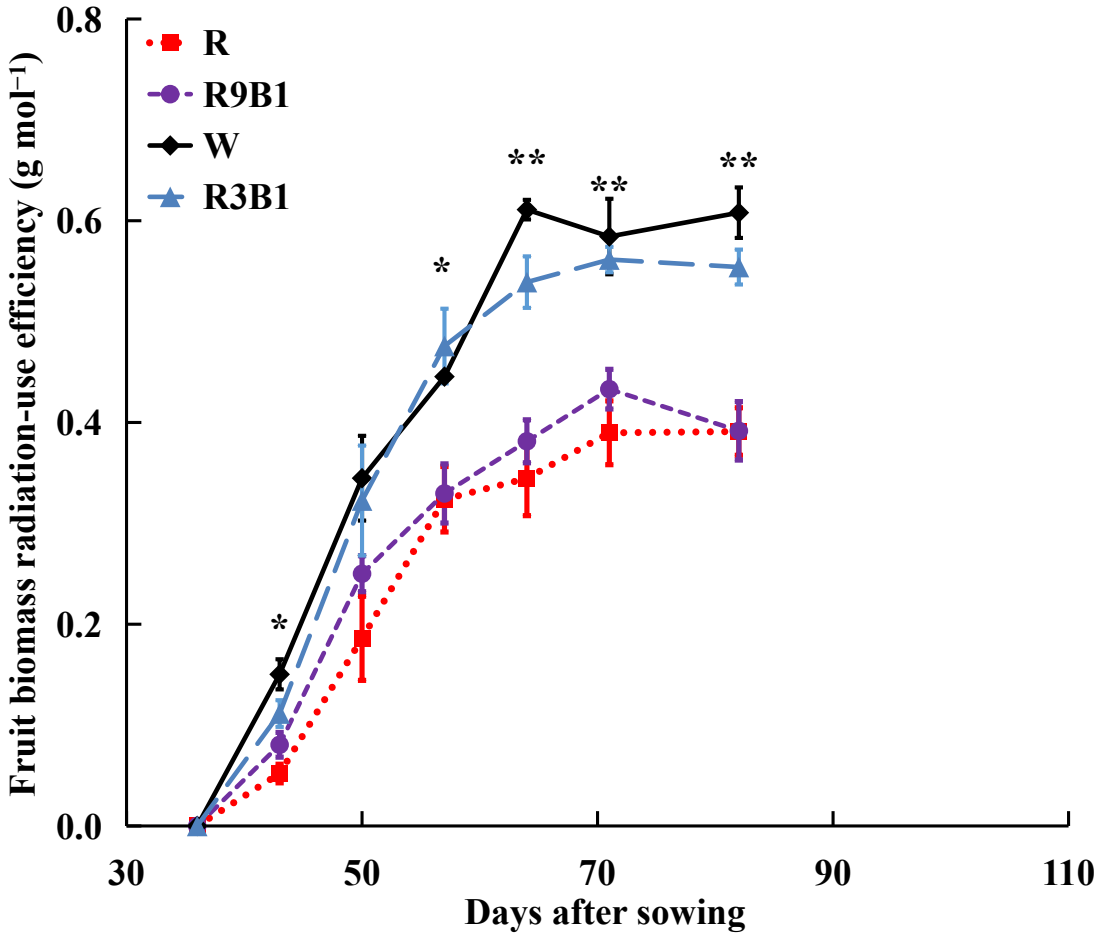

Figure 4.11. Effect of light quality on fruit biomass radiation-use efficiency (FBRUE) over time in 'Micro-Tom' ['Micro-Tom']. Error bars represent ± standard error. * and ** indicates significant difference among the treatments based on Tukey−Kramer's test at $p < 0.05$ and $p < 0.01$ (n = 3). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

In Rejina, FBRUE was significantly affected by light quality from 70 DAS (Figure 4.12). From 70 DAS, FBRUE in W was significantly higher than others. The highest RUE and F_{fruits} led to the highest FBRUE. The FBRUE of Micro-Tom was higher than that in Rejina in the same light quality treatment because of higher RUE rather than higher F_{fruits}. Previous studies reported that the FBRUE of tomatoes cultivated in the controlled environment systems at harvest was 0.2–0.36 g mol^{-1} (Wheeler et al., 2008; Goto, 2011; Li et al., 2019). In the present study, the FBRUE at harvest in Micro-Tom

was 0.39–0.61 g mol^{-1} (Figure 4.11) and was higher than those in the previous studies. The FBRUE at harvest in Rejina was 0.21–0.51 g mol^{-1} (Figure 4.12) and slightly higher than those in the previous studies. This shows that the environmental control and variety selection like Micro-Tom used in the present study improved the FBRUE of tomatoes.

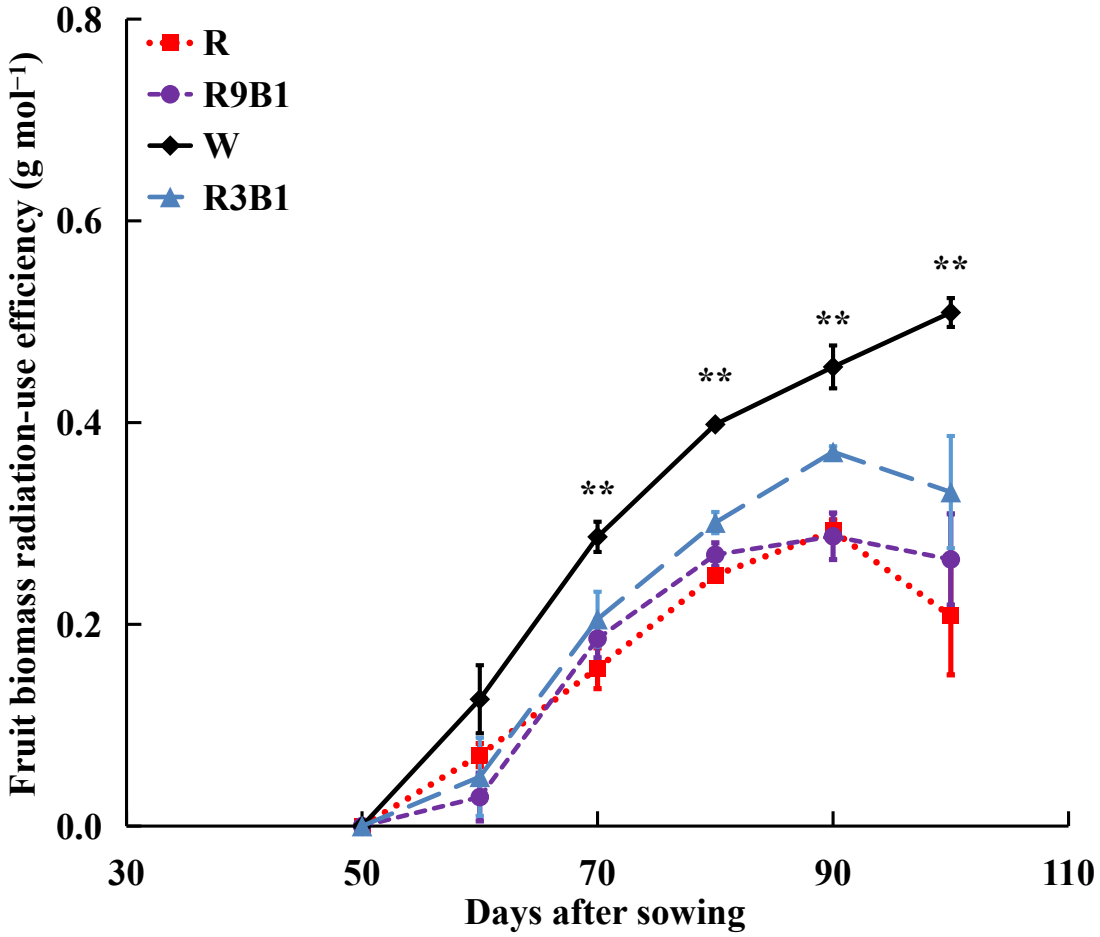

Figure 4.12. Effect of light quality on fruit biomass radiation-use efficiency (FBRUE) over time in 'Rejina' ['Rejina']. Error bars represent ± standard error. ** indicates significant difference among the treatments based on Tukey−Kramer's test at $p < 0.01$ (n = 3). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

4.3.6. Fruit quality, yield and light electric energy productivity

In Micro-Tom, fruit dry matter ratio in W was significantly higher than that in R and Brix in W was significantly higher than that in R3B1 at 82 DAS (Table 4.7). There was no significant difference in other growth items among the treatments. The lowest Pn in R (Figure 3) led to the lowest fruit dry weight which caused the lowest fruit dry matter ratio. However, red light might improve content of soluble sugars in tomato (Erdberga et al., 2020). This also correspondences with the research which showed that an increased red to blue ratio enhanced the tomato glucose and fructose contents and sugar/acid ratio (Thwe et al., 2020). Therefore, the fruit Brix in R3B1 rather than R was the lowest (Table 4.7). In W, the fruit dry weight and fruit dry matter ratio were the highest. In addition, the white light contains far-red radiation which can increase fruit sugar concentration (Ji et al., 2020) and upregulated the expression of genes associated with both sugar transportation and metabolism, such *HY5* (van Gelderen et al., 2018), sucrose transporters *SWEET11* and *SWEET12* (Chen et al., 2016). Therefore, the Brix in W was the highest.

Table 4.7. Effects of light qualities on the number of fruits, fruit fresh and dry weights, fruit dry matter ratio, and fruit quality in 'Micro-Tom' 82 DAS and in 'Rejina' 100 DAS. Each value represents the mean ± standard error. Different letters indicate significant differences at the $p < 0.05$ level among light quality treatments with Tukey−Kramer's test. Each value of the number of fruits, fruit fresh and dry weight, and fruit dry matter ratio represents a mean of three values. There were 6−9 fruits sampled in each treatment for fruit quality. R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

Cultivar	Treatment	Number of fruits	Fruit fresh weight (yield, g)	Fruit dry weight (g)	Fruit dry matter ratio (%)	Brix (%)	Acidity (%)	Brix/acidity
Micro-Tom	R	15.0 ± 1.2	79.1 ± 8.1	6.2 ± 0.9	7.7 ± 0.4 b	5.4 ± 0.1 ab	1.2 ± 0.1	4.7 ± 0.3
	R9B1	12.8 ± 1.3	72.6 ± 7.8	5.9 ± 0.5	8.3 ± 0.4 ab	5.3 ± 0.2 ab	1.2 ± 0.1	4.5 ± 0.4
	W	14.3 ± 1.9	66.8 ± 10.4	6.4 ± 1.0	9.6 ± 0.1 a	5.7 ± 0.4 a	1.3 ± 0.1	4.5 ± 0.3
	R3B1	15.8 ± 1.5	90.5 ± 4.7	7.7 ± 0.4	8.5 ± 0.2 ab	4.8 ± 0.2 b	1.3 ± 0.1	4.1 ± 0.6
Rejina	R	36.3 ± 2.2	212.3 ± 73.4	13.3 ± 4.2	6.5 ± 0.4	5.5 ± 0.1	0.7 ± 0.1	8.5 ± 0.8
	R9B1	34.7 ± 5.4	245.9 ± 77.4	16.2 ± 5.2	6.5 ± 0.1	5.5 ± 0.2	0.7 ± 0.1	7.9 ± 0.6
	W	31.0 ± 5.5	339.5 ± 42.3	23.3 ± 3.2	5.8 ± 0.2	5.9 ± 0.2	0.6 ± 0.0	10.6 ± 0.8
	R3B1	30.0 ± 5.6	300.2 ± 87.0	20.3 ± 5.6	6.8 ± 0.1	5.8 ± 0.1	0.7 ± 0.0	8.1 ± 0.5

In Rejina, there were no significant differences in the number of fruits, fruit fresh and dry weight, fruit dry matter ratio, and fruit quality among all treatments at 100 DAS.

The number of fruits, fruit fresh and dry weight of one plant in Micro-Tom were less than those in Rejina until harvest (Table 4.7).

There was no significant difference in the yield per unit ground area among light treatments in the two cultivars (Table 4.8). However, the yield per unit PLA in W was significantly higher than those in R and R9B1 in Rejina. The power of white lamps was the lowest. In the red and blue light LED lamps, higher proportion blue light led to higher power and light electric energy consumption. Moreover, the maximum value in R3B1 in Rejina of the light electric energy consumption during a growth cycle was almost twice the minimum value in W in Micro-Tom among eight treatments. The light electric energy productivities were the highest in W and the lowest in R9B1 in the two cultivars among all light treatments. The light electric energy productivity in Micro-Tom was higher than Rejina under the same light quality condition.

Table 4.8. Effects of light qualities on the yield, power of lamps during experiments, light electric energy consumption during a growth cycle and light electric energy productivity in 'Micro-Tom' 82 DAS and in 'Rejina' 100 DAS. FW is fresh weight (g); PLA is projected leaf area (m^{-2}). Each value in yield represents the mean ± standard error. Different letters indicate significant differences at the $p < 0.05$ level among light quality treatments with Tukey−Kramer's test (n = 3−6). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

Cultivar	Light quality	Yield[1] (kg FW m^{-2} ground area[2])	Yield[3] (kg FW m^{-2} PLA)	Power of lamps during experiments[4] (W/m^2 ground area)	Light electric energy consumption during a growth cycle[5] (MJ/m^{-2} ground area)	Light electric energy productivity[6] (g FW/MJ)
Micro-Tom	R	18.9 ± 1.9	3.8 ± 0.4	196.4	815.7	29.1
	R9B1	17.3 ± 1.9	3.8 ± 0.4	244.7	946.4	22.2
	W	15.9 ± 2.5	4.6 ± 0.7	144.9	676.3	31.3
	R3B1	21.5 ± 1.1	5.0 ± 0.3	285.0	1055.8	24.3
Rejina	R	7.9 ± 2.7	2.2 ± 0.8 b	196.4	1032.8	12.1
	R9B1	9.2 ± 2.9	2.7 ± 0.8 b	244.7	1171.9	11.5
	W	12.6 ± 1.6	9.9 ± 1.2 a	144.9	884.5	24.9
	R3B1	11.2 ± 3.2	6.1 ± 1.8 ab	285.0	1288.2	12.3

1: The values are the fresh weight of tomato fruits per unit of ground area at 82 DAS in 'Micro-Tom' and 100 DAS in 'Rejina', respectively.
2: Ground area is defined as the cultivation area under 8 lamps used in each treatment, which is 0.6 m × 1.3 m = 0.78 m^2.
3: The values are the fresh weight of tomato fruits per unit of projected leaf area at 82 DAS in 'Micro-Tom' and 100 DAS in 'Rejina', respectively.
4: The experiment period is 36−82 DAS in 'Micro-Tom' and 50−100 DAS in 'Rejina', respectively.
5: A growth cycle is 0−82 DAS in 'Micro-Tom' and 0−100 DAS in 'Rejina', respectively.
6: Light electric energy productivity (Kozai, 2018) is the yield of tomatoes (g) per unit electric energy consumption for lighting (MJ).

4.4. Conclusion

This study showed that FBRUE of Micro-Tom and Rejina increased with an increase in blue light proportion from 0 to 25% at 300 μmol m^{-2} s^{-1} PPFD under red and blue LED light. However, FBRUE values of two dwarf tomato cultivars were the highest under white LED light. FBRUE increased because of the increased RUE and F_{fruits}. White light and high blue light proportion led to high RUE because of higher Pn and high absorbance of top leaves. RUE, FBRUE and light electric energy proclivity were the highest in W. Therefore, W is recommended for 'Micro-Tom' and 'Rejina' cultivation to improve FBRUE and RUE at the reproductive growth stage. The results of this study would be helpful in efficient tomato production in PFALs and may help elucidate the effects of light quality on FBRUE of dwarf tomatoes under LED light.

4.5. Supplementary materials

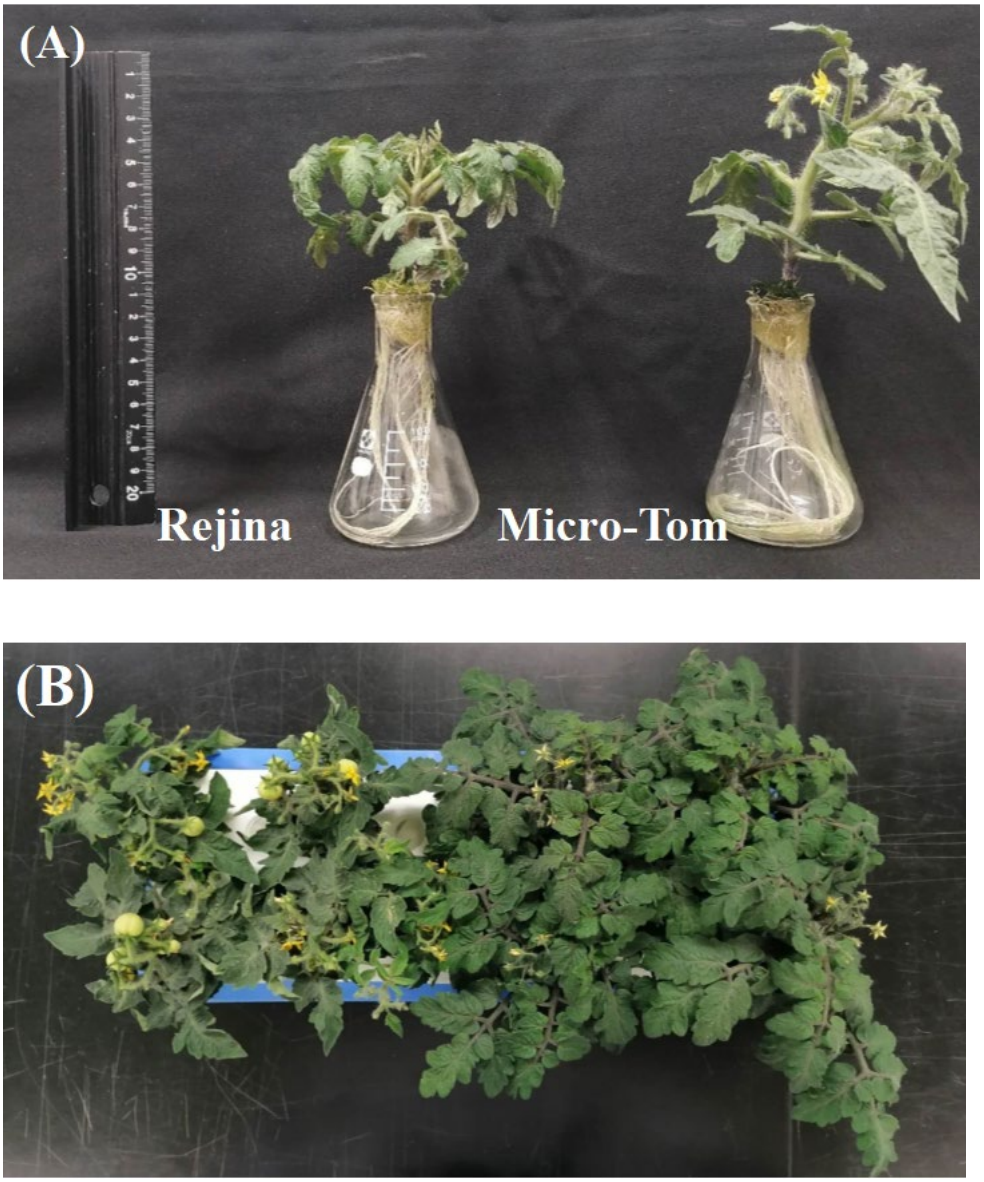

Figure S4.1. Micro-Tom and Rejina plants at 36 DAS (A) and 52 DAS (B) under white LED light.

Table S4.1. Effects of light qualities on the number of fruits, fruit fresh and dry weigh in ‘Micro-Tom’ 71 DAS and in ‘Rejina’ 70 DAS. Each value represents the mean ± standard error. Different letters indicate significant differences at the $p < 0.05$ level among light quality treatments with Tukey−Kramer’s test (n = 3−4). There were 6−9 fruits sampled in each treatment for fruit quality. R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

Cultivar	Light quality	The number of fruits	Fruit fresh weight (g)	Fruit dry weight (g)	Yield (g FW m^{-2})
Micro-Tom	R	16.3 ± 1.8	49.4 ± 8.0	4.0 ± 0.8	11.8 ± 1.9
	R9B1	17.0 ± 1.2	55.5 ± 6.0	4.8 ± 0.3	13.2 ± 1.4
	W	14.7 ± 0.7	50.2 ± 9.2	4.3 ± 0.8	11.9 ± 2.2
	R3B1	17.3 ± 4.3	69.6 ± 11.8	6.1 ± 0.9	16.6 ± 2.8
Rejina	R	31.3 ± 5.2	33.0 ± 2.0 b	4.7 ± 1.1 b	2.7 ± 0.6 b
	R9B1	29.7 ± 2.8	73.0 ± 17.4 ab	4.7 ± 0.6 b	2.5 ± 0.3 ab
	W	35.0 ± 4.0	135.7 ± 21.3 a	9.2 ± 1.5 a	5.1 ± 0.8 a
	R3B1	36.0 ± 4.7	90.9 ± 7.6 ab	6.0 ± 0.4 ab	3.4 ± 0.3 ab

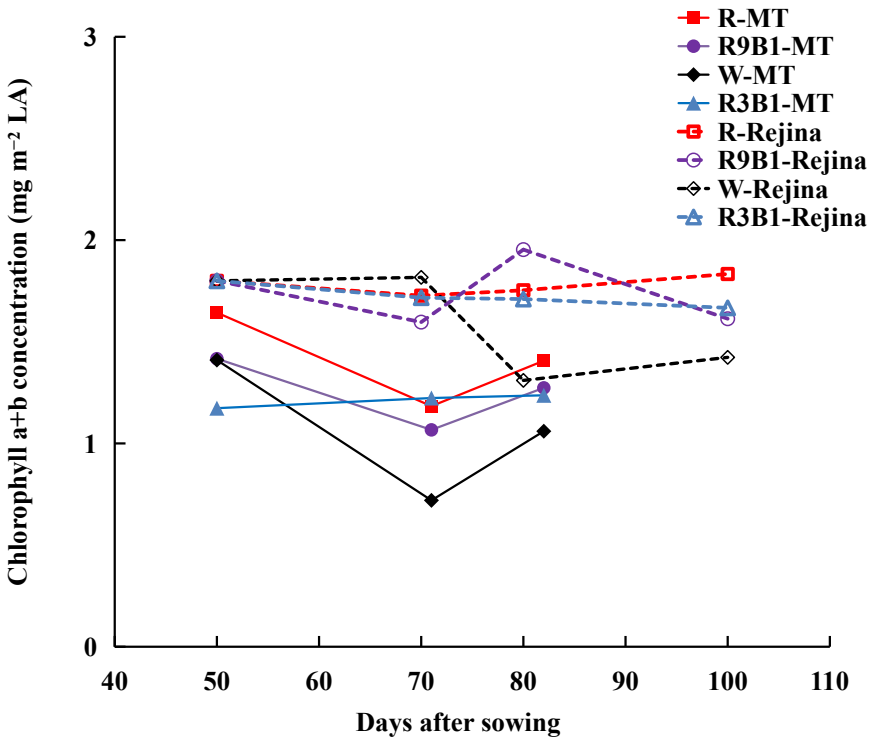

Figure S4.2. Effects of light quality on chlorophyll concentrations per unit of leaf area (LA) of leaves in the two cultivars. Solid point represents the average value of three plants in each treatment (n = 3). R: red light; R9B1: red/blue ratio = 9; W: white light; R3B1: red/blue ratio = 3.

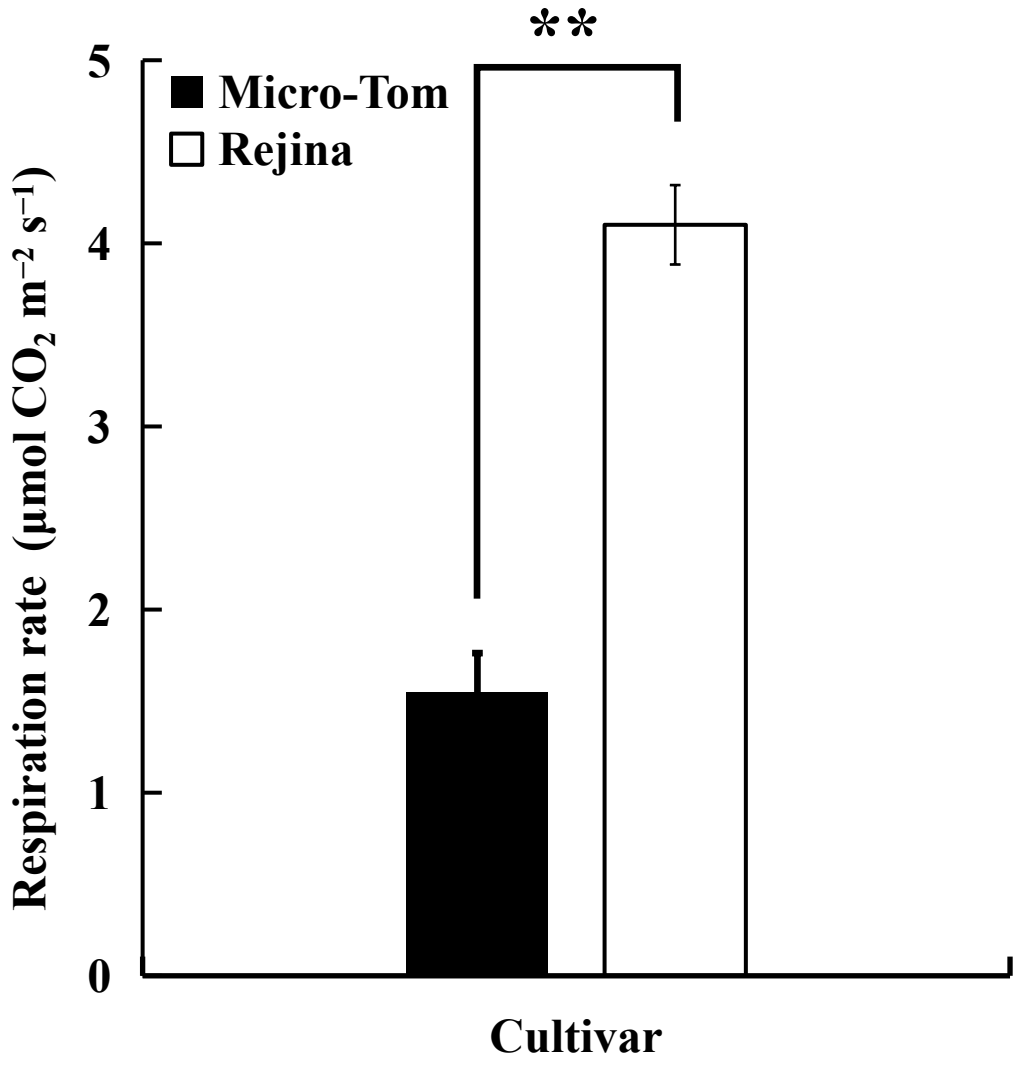

Figure S4.3. Respiration rates of leaves in two tomato cultivars. Respiration rates were measured at 50 DAS in W treatment in 'Micro-Tom' and at 51 DAS in 5000K treatment conducted by Momata san in 'Rejina', respectively. ** indicates significant difference among the treatments based on Student's test at $p < 0.01$ (n = 4).

CHAPTER 5.

Conclusions

5.1. Summary

This thesis aimed to investigate the effects of PPFD and light quality on growth, RUE, FBRUE, and yield of dwarf tomatoes under LED light to develop a strategy for controlling light conditions of dwarf tomatoes during the vegetative and reproductive growth stages to improve RUE and FBRUE.

In Chapter 2, the effects of PPFD and light quality on growth and RUE of dwarf tomatoes were investigated and the suitable PPFD and light quality for improving the RUE at the vegetative growth stage were determined. The results clearly demonstrated that higher PPFD led to higher dry mass and lower specific leaf area (SLA), but it did not affect the stem length. Furthermore, high PPFD increased the net photosynthetic rate (Pn) of individual leaves but decreased RUE. A higher blue light proportion inhibited dry mass production with the same intercepted light because the leaves under high blue light proportion had low Pn and photosynthetic quantum yield. In conclusion, 300 μmol m^{-2} s^{-1} PPFD and R9B1 are the recommended proper PPFD and light quality, respectively, for 'Micro-Tom' cultivation at the vegetative growth stage to increase the RUE.

In Chapter 3, the effects of PPFD on growth, RUE, FBRUE, source strength (S_{source}) and fruit sink strength ($S_{fruit\text{-}sink}$) of dwarf tomatoes were investigated and the suitable PPFDs for improving FBRUE and yield at the vegetative growth stage were determined, respectively. The results evidently demonstrated that a higher PPFD led to higher fresh and dry weights of plants and lower SLA. FBRUE and RUE were the highest under 300 μmol m^{-2} s^{-1}. FBRUE decreased because of the decreased RUE and the fraction of dry mass portioned to fruits (F_{fruits}) with increased PPFD from 300 to 700 μmol m^{-2} s^{-1}. Higher PPFD (500 and 700 μmol m^{-2} s^{-1}) led to lower RUE owing to lower light absorptance, photosynthetic quantum yield, and photosynthetic capacity of the leaves. PPFD did not affect the potential growth rate of individual fruits but the number of fruits. In addition, S_{source} and $S_{fruit\text{-}sink}$ increased with PPFD. Higher PPFD increased yield and fruit quality. In conclusion, 300 and 700 μmol m^{-2} s^{-1} PPFDs are

recommended for ‘Micro-Tom’ cultivation to improve the FBRUE and yield at the reproductive growth stage, respectively.

In chapter 4, the effect of light quality on FBRUE of two dwarf tomato cultivars (‘Micro-Tom’ and ‘Rejina’) at the reproductive growth stage were investigated. The results showed that FBRUE of Micro-Tom and Rejina increased with an increase in blue light proportion from 0 to 25% at 300 μmol m^{-2} s^{-1} PPFD under red and blue LED light. However, FBRUE values of two dwarf tomato cultivars were the highest under white LED light. FBRUE increased because of the increased RUE and F_{fruits}. White light and high blue light proportion led to high RUE because of higher Pn and high absorbance of top leaves. RUE, FBRUE and light electric energy proclivity were the highest in W. Therefore, W is recommended for ‘Micro-Tom’ and ‘Rejina’ cultivation to improve FBRUE and RUE at the reproductive growth stage.

The results of these studies demonstrated that RUE and FBRUE can be improved by regulating PPFD and light quality. The effects of PPFD and light quality on RUE and FBRUE of dwarf tomatoes were elucidated. The results of our study would be helpful in efficient tomato production in PFALs.

5.2. Suggestions for future research

Firstly, there are many dwarf tomato cultivars other than ‘Micro-Tom’. However, only one cultivar was used in this thesis. It is necessary to test more cultivars and seek cultivars suitable for production in a PFAL with high yield and quality. In addition, the differences in yield and RUE between dwarf tomato and common tomato cultivars in a PFAL should be systematically determined and reviewed based on the experiments using various cultivars in the future.

In this thesis, the axillary buds were pruned. Pruning costs a lot of labor. If the axillary buds are not pruned, the leaf area and number of fruits will increase as well as fresh and dry weights of single fruit will decrease. RUE would be changed even the plants are cultivated in the same environment. In addition, the axillary buds will increase workload for harvest. Then, installation of a harvest machine/robot is considered desirable for tomato production in a PFAL in the future. Therefore, the effect of pruning axillary buds on workload for harvest as well as RUE, FBRUE, and fruit quality should be determined in the future.

Light quality regulation includes not only these of red and blue lights but also the regulation of other light qualities like far-red light, green light, UV light. More detailed researches about the effects of light quality on RUE and FBRUE of tomatoes in a PFAL should be discussed in the future.

Some dwarf tomato cultivars are determinate tomatoes and produce fruits are on the top of canopy (terminal end). The PPFD on the surface of these fruits is higher than that on the leaves. However, the photosynthetic rate of tomato fruits is not as high as leaves (Carrara et al., 2001; Lytovchenko et al., 2011). Owing to shading by these fruits, leaves beneath the plant canopy suffer from low PPFD conditions when the light direction is downward from the top. Therefore, changing the light direction may increase the PPFD on the leaves beneath the plant canopy and enhance the RUE of

whole canopy.

In Chapter 3, 300 μmol m^{-2} s^{-1} PPFD is recommended to improve FBRUE and RUE. A PPFD of 700 μmol m^{-2} s^{-1} is recommended to improve yield and fruit quality. Therefore, dynamic PPFD management based on the source-sink relationship might be suitable for balancing RUE and yield in the future.

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ACKNOWLEDGEMENTS

やったー！　明らかに、すべて自分でやったわけではありません。

I want to thank everyone who helped me in the past three and half years.

Firstly, the person who I want to thank most is my supervisor, Dear Eiji Goto sensei. I still remember the first time I saw the English first name of Goto sensei, my first reaction was ‘GO TO’. Where should I go to? After three and half years, the answer comes. Goto sensei opened a science door for me and leads me to a ‘research’ load. I learn a lot from Goto sensei and I think one sentence from an ancient Chinese book ‘Analects’ (論語) to show my feelings to Goto sensei. It is ‘仰之弥高。鑽之弥堅。瞻之在前。忽焉在後。夫子循循然善誘人。博我以文。約我以礼。欲罷不能。既竭吾才。如有所立卓爾。’. He showed me not only the knowledge but also the method. He is erudite and interesting. I remembered he draw a figure showed that if one person does not wear a mask, the person should be directly thrown into the other side of the earth through the induction device installed in front of the convenience store at the beginning of COVID-19. I think he has a lot of blue-sky thinking thanks to the long commute. I could not have wished for a better Lab. and supervisor.

In our Lab., everyone is so nice! I see a lot of good characteristics such as hardworking, brave, persistent, youthful, enthusiastic, united and hopeful. I spend a happy and meaningful time in my life. I love my Lab. members!

I also thank Shoko Hikosaka sensei. As a mother of four kids, she is gentle and affectionate to students. I admire her for balancing life and work so well. She told the students a lot of details and safety matters very well. In addition, I was so surprise when I talked with her for the first time. Because her Japanese was so clear and easy to understand, and just like Japanese textbook. I still remember her first question to me was that why do you come to Japan to study, very impressive.

I enjoy talking with Hideo Yoshida sensei very much. He became the assistant professor at the right time when I entered the Lab., and we shared the same welcome party together. I called it ‘縁’ . As a brilliant and young sensei, he works very hard.

Sometimes I think he has some magic to fix a lot of experimental tools. Thank him for telling me job information in Japan. In addition, I spent a meaningful time with him during the 2021 AGHPF conference. I hope we can eat delicious Chinese food together in the near future.

In our Lab., there are more than 20 students. It is a big family! I like cooking activities in Planto, softball game, campus festival, BBQ, cherry blossom viewing party and drink party. These beautiful memories united everyone in this family. I would like to thank my Lab. members for their help, support and these memories.

I want to thank my parents. They support and encourage me as always. I feel so sorry that I haven't been home for three and half years due to COVID-19. I understand their love and worries. I love you forever, 爸爸妈妈.