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Tomato Fruit Growth and Nutrient Accumulation in Response to Blue and Red Light Treatments during the Reproductive Growth Stage

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Abstract: Tomatoes are an important fruit consumed worldwide. Within protected cultivation environments, artificial light using energy-efficient light-emitting diodes can be applied in tomato production as an effective way to improve productivity and nutritional value. Several studies have investigated the effects of supplementing artificial light on various aspects of tomato growth, encompassing flowering, fruit development, ripening, and nutritional composition. However, the outcomes of previous studies offer inconclusive insights into whether the observed impacts on tomato growth have resulted from the provision of additional photons or discrepancies in the spectral distribution of light during artificial light supplementation. Within this context, this study aimed to specifically explore the independent effects of monochromatic blue and red light, along with their dichromatic mixture (blue + red), on fruit growth and nutrient accumulation in comparison with multispectral white light. These four different light treatments were implemented after anthesis under the same photosynthetic photon flux density to mitigate possible variabilities arising from different light intensities and originating during the vegetative growth stage. As a result, under the same light intensity conditions, red and blue + red light irradiance during the reproductive growth stage delayed fruit ripening by up to 4.33 days compared to white light. Regarding fruit productivity, the fresh weight of fully ripe tomato fruit in the blue, red, or blue + red light treatment groups was not different from that in the white-light treatment group, whereas the blue light treatment significantly reduced the number of fruits in the plant. Finally, nutrient content, including soluble sugars, lycopene, and β-carotene, significantly increased by 10.0%, 27.1%, and 65.2%, respectively, in the blue compared to the white light-irradiated group. This study demonstrated that the application of distinct light spectra during the reproductive growth phase could have varying impacts on tomato fruit development and nutrient accumulation. By integrating our findings with results from prior studies, a more efficient light intervention strategy could be developed to effectively regulate traits of tomato fruit within an indoor production system.

Keywords: β-carotene; fruit development; light modulation; light intensity; light quality; lycopene

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1. Introduction

Light is a major factor determining plant growth and development. In nature, owing to the wave-particle duality of light, plants respond simultaneously to the number of photons (light intensity) and spectral distribution of light (light quality). Numerous studies have investigated the effects of light intensity, light quality, and their interactions on a wide

range of physiological and biochemical processes, such as photosynthesis, photomorphogenesis, and metabolism [1–5]. In addition, the supplementation and modulation of light conditions have been utilized as effective ways to improve crop productivity, nutritional value, pre/postharvest quality, and biotic stress tolerance [6–13].

Tomatoes are important fruits consumed worldwide and are a major source of phytonutrients and dietary antioxidants [14,15]. To meet global demand, the tomato cultivation area has increased by approximately 23% during the last two decades [16]. Greenhouse production continues to increase because controllable environmental conditions enable year-round production with higher yields and consistent quality control. Light conditions are controllable factors that enhance the tomato production efficiency in indoor production systems [9,17]. The use of light-emitting diodes (LED) as artificial light sources further increases the feasibility of light intervention practices because of their high energy efficiency and the controllability of light intensity and quality [13,18–20].

Several studies have investigated the effects of light treatment on tomato growth, flowering, fruit development, ripening, nutritional composition, and postharvest fruit quality. The overall fruit yield and quality can be improved with either over-canopy or intra-canopy supplemental radiation [8,10,21]. In particular, supplementation with monochromatic blue light, red light, or a mixture of blue and red light using LEDs appeared to accelerate the ripening process and improve the nutritional value [7,8,22]. For example, in a recent study, intermittent or continuous blue light supplementation facilitated fruit ripening up to 8 days earlier and enhanced the content of various phytonutrients, including lycopene, compared with natural light conditions [7]. Another study showed similar results: that intra-canopy supplementation with blue or red light increased the fruit ripening speed and lycopene and β-carotene content [23]. However, these previous studies remain inconclusive as to whether the impact on fruit ripening and nutrient accumulation is due to increased light intensity or differences in light quality among the light treatment group. In the above- mentioned studies, indeed, calculated amounts of photons additionally provided into the monochromatic light treatment group were 4.320 and 5.184 $mol \cdot m^{-2} \cdot day^{-1}$ during the experimental periods (for 42 and 25 days, respectively), whereas the control group under multispectral light conditions did not receive additional photons. In order to clarify this issue, this study investigated the sole effects of light quality on tomato fruit development and maturation by treating with the same intensity of light during the reproductive growth period. Moreover, nutritional characteristics, including representative health-promoting phytonutrients (lycopene, β-carotene), were analyzed and compared in fully mature tomatoes grown under different light quality conditions with the same light intensity.

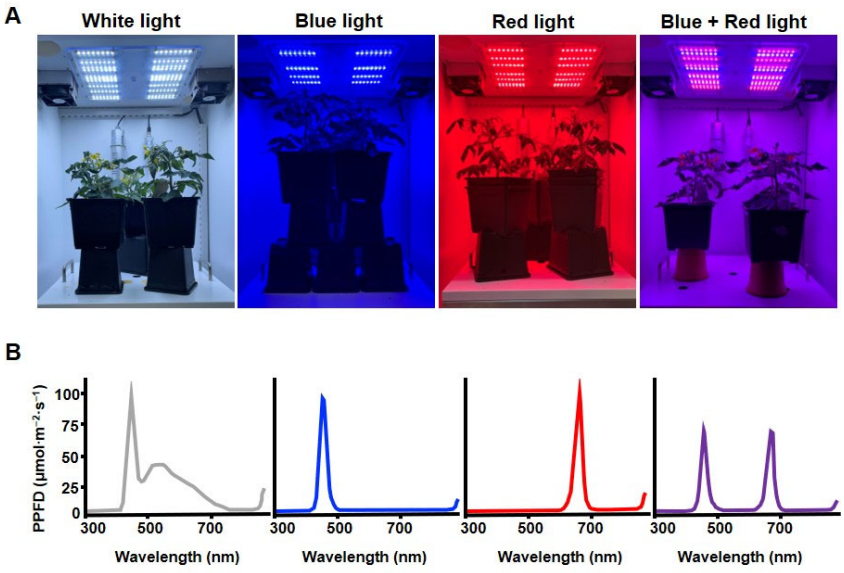
2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Solanum lycopersicum cv. Micro-Tom was used in this study. Seeds were placed on a Petri dish with moist germination paper and germinated for 5 days in a plant growth chamber under 24 ± 2 °C, 60 ± 5% relative humidity, and dark conditions. After radicle and cotyledon emergence, individual seedlings were transferred to a 1 L pot (width 10 cm × vertical 10 cm × height 10 cm) filled with autoclaved soil (Hungnong Bio, Bayer Korea Co., Seoul, Republic of Korea). The chemical properties of soil were as follows; pH 6.6, organic matter 110.6 $g \cdot kg^{-1}$, cation exchange capacity 29.0 $cmol \cdot kg^{-1}$, NH_3^- 13.4 $mg \cdot kg^{-1}$, NH_4^+ 140.1 $mg \cdot kg^{-1}$, P_2O_5 257.4 $mg \cdot kg^{-1}$, exchangeable K 5.4, Ca 4.9, and Mg 3.1 $cmol \cdot kg^{-1}$. The transferred plants were grown for 3 weeks until the developmental stages were reached 5 days after anthesis (DAA). For this period, plant growth was carried out in a growth chamber under 24 ± 2/18 ± 2 °C (day/night), 60 ± 5% relative humidity, 14 h photoperiod, and photosynthetic photon flux density (PPFD) 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light intensity. A cool white fluorescent lamp with peak wavelengths of 436 nm and 543 nm was used as the light source. Plants were irrigated with 100 mL of tap water every 10 days.

2.2. Experimental Design and Light Treatments

Five DAA-old plants were selected and moved to individual plant growth chambers equipped with controllable LED lights to investigate the effects of light quality on fruit development after anthesis. Six plants at identical growth stages were randomly placed in each growth chamber (completely randomized design with six biological replicates). Four light treatments were used: full-spectrum white light, blue light with a peak wavelength of 454 nm, red light with a peak wavelength of 658 nm, and a 1:1 mixture of blue + red light (blue + red). The relative number of photons in a 100 nm bandwidth for each light treatment is shown in Figure 1. Except for the spectral distribution of light, the other environmental conditions were identical across the treatment groups. Light intensity was set to PPFD 300 μmol· m^{-2}·s^{-1} at the canopy level by adjusting the output of LED light and the distance between the light source and the top of the plant canopy. To maintain the homogeneity of light conditions, the light intensity and spectral distribution of each treatment were measured and monitored during the experimental period using a quantum sensor (LI-250; LI-COR Bioscience, Lincoln, NE, USA), and plants were relocated in the chamber if necessary. Plant growth occurred until harvest time (82 DAA) under 24 ± 2/18 ± 2 °C (day/night), 14 h photoperiod, and ambient humidity conditions. Plants were sub-irrigated every 7–10 days.



C

	PPFD (μmol·m⁻²·s⁻¹) in a bandwidth of 100 nm			
Wavelength	White (%)	Blue (%)	Red (%)	Blue+Red (%)
400–499 (nm)	96 (32)	285 (95)	6 (2)	132 (44)
500–599 (nm)	126 (42)	9 (3)	9 (3)	6 (2)
600–699 (nm)	78 (26)	6 (2)	285 (95)	162 (54)
Total	300 (100)	300 (100)	300 (100)	300 (100)

Figure 1. Different light-quality treatments during the reproductive growth stages of tomato. (**A**) Four different light-quality treatments conducted under a controlled environment using a growth chamber. In each light treatment group, light intensity was set to PPFD 300 μmol·m^{-2}·s^{-1} at the canopy level by adjusting the LED light power and the distance between the light source and the top of the plant canopy. (**B**) Spectral distribution of each light. (**C**) Light intensity in a 100 nm bandwidth for each light treatment. PPFD: photosynthetic photon flux density.

2.3. Investigating Tomato Fruit Development and Ripening

Tomato fruit development was divided into immature and mature stages (Figure 2). After the fruit set, fruits that increased in size in response to cell division and enlargement were defined as immature stage fruits, whereas mature stage fruits reached their full size and displayed changes in surface color. During the mature stage, fruit ripening occurred and it was further classified into six stages, from mature green (MG) to red ripe (RR), based on fruit surface color (Figure 2). The fruit ripening stages were determined using the USDA color classification standard (United States Standards for Grades of Fresh Tomatoes, USDA, 1991) [24]. To investigate the effects of light quality on fruit development and ripening, flowers at anthesis (0 DAA) were tagged for each plant, and the number of days required to reach the MG and RR stages were recorded for each light treatment regime. In addition, at 82 DAA, the number of fruits under either the immature or mature stage was counted per plant, and among the mature stage fruits the fresh weight of the RR stage fruit was measured as a fruit production parameter for each light condition.

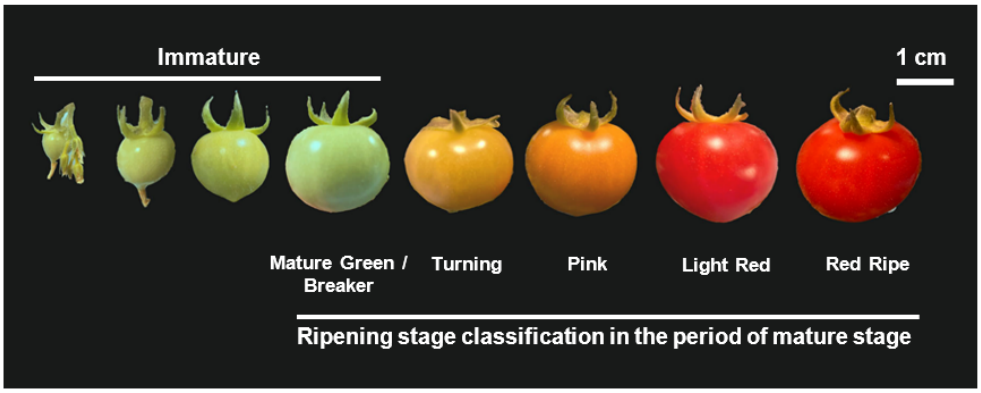


Figure 2. Determination and classification of the development and ripening stages of tomato fruit. The fruit developmental stages are divided into immature and mature stages. The fruit ripening stages within the mature stage are divided into six stages: mature green, breaker, turning, pink, light red, and red ripe. The scale bar indicates 1 cm.

2.4. Investigating the Nutritional Characteristics of Tomato Fruits

The nutritional characteristics were investigated in the RR stage fruits harvested at 82 DAA from each light treatment group. All of the fruit samples were immediately freeze-dried after harvest and then ground into a powder before analysis. One gram of the powder sample was mixed with 9 mL of distilled water and filtered through 5 µm pore qualitative filter paper. pH and total soluble solid content (°Brix) were measured in filtered solution, as previously described [25], using a pH meter and a refractometer, respectively.

The total soluble sugar content was determined using the Kohyama and Nishinari method [26]. Powder samples (500 mg) were mixed with 8 mL of ethanol (80%, *v*/*v*) and then incubated at 80 °C for 40 min in a water bath. The supernatant was mixed with one-quarter of distilled water and diluted with sulfuric acid anthrone. The solution was boiled for 10 min, and its absorbance was measured at 625 nm using a spectrophotometer [7].

The total soluble protein content was determined with the Bradford method, using bovine serum albumin as a standard. Powder samples (500 mg) were mixed with 8 mL of distilled water and subsequently subjected to centrifugation at 3000 g for 10 min at 4 °C. Following centrifugation, 0.2 mL of the resulting supernatant was combined with 0.8 mL of distilled water, and then mixed with 4 mL of Coomassie Brilliant Blue G-250 solution. The sample was incubated for 5 min, and its absorbance was measured at 595 nm using a spectrophotometer [7].

The lycopene and β-carotene content was determined as previously described, with slight modifications [27]. Powder samples (50 mg) were mixed with 1 mL of hexane and ethanol mixture (1:1 in volume), and ultrasonic extraction was performed for an hour

at 30 °C. After centrifugation, the supernatant was filtered through a 0.45 µm cellulose membrane syringe filter. HPLC analysis was carried out using an Agilent (Palo Alto, CA, USA) series 1260 liquid chromatograph and a YMC-carotenoid C30 column packed with 5 µm particles (4.6 × 250 mm) in a 30 °C column oven. Methanol:methyl tert-butyl ether:water (81:15:4) and methanol:methyl tert-butyl ether:water (7:90:3) were used as mobile phase solvents A and B, respectively. The injection volume was 20 µL. The flow rate was 1.0 mL·min^{-1}, and UV detection was performed at 450 nm.

2.5. Statistics Analysis and Graph Visualization

t-tests were performed for each light treatment group (blue, red, or blue + red) against the white light treatment group (n = 6) using the R software (Version 4.2.1). In addition, graph visualization was performed using GraphPad software (Prism 9.5.1).

3. Results and Discussion

3.1. Effects of the Different Spectral Distributions of Light on Tomato Fruit Development and Ripening after Anthesis

To the best of our knowledge, this is the first study to investigate the sole effects of light quality on tomato fruit maturation and ripening by treating with the same intensity of light with different spectra only after anthesis. As shown in Figure 3A, the period of the immature stage (time required to reach the MG stage from anthesis) under monochromatic blue- or red-light irradiance conditions was not different from that under white light (full spectrum light similar to natural light) conditions. However, blue- and red-light irradiance at a 1:1 ratio (blue + red) significantly delayed tomato fruit maturation by 3.5 days compared to white light. This suggests that blue and red light interact in the regulation of fruit setting and maturation.

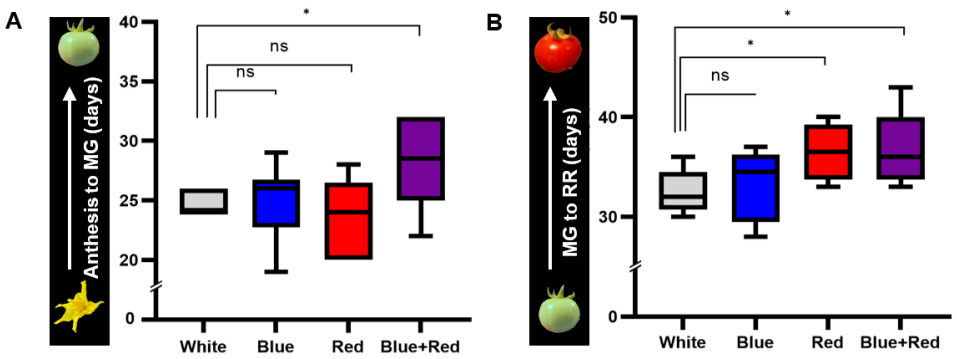


Figure 3. Effect of different light treatments during the reproductive stage on tomato fruit development and ripening. (**A**) Required time for reaching the mature green (MG) stage from anthesis in each light treatment group. (**B**) The duration of tomato fruit ripening from mature green (MG) to red ripe (RR) stage in each light treatment group. The square box means the value from the lower quartile of 25% (Q1) to the upper quartile of 75% (Q3) of the inter-quartile range (IQR), and the line inside the box is the median (50%). The upper and lower whisker lines outside the box represent the maximum and minimum values. T-tests were performed for each light treatment group (blue, red, or blue + red) against the white light treatment group (n = 6). Symbols denote statistical significance (n.s. = not significant; * = $p < 0.05$).

During the mature stage period, fruit ripening from the MG to RR stage was significantly delayed by 4.00 and 4.33 days under red and blue + red light conditions, respectively, whereas blue light did not affect the duration of the fruit ripening stage, compared to white light (Figure 3B). Previous studies have indicated that supplementation with blue or red light facilitates tomato fruit ripening [7,23,28,29]. However, as mentioned in the introduction, this might be attributed to additional irradiated photons rather than to different light spectra. This previous study used the same light intensity with different spectra, similar to ours, but the light treatment was conducted from the seedling stage to the harvesting

time, unlike the present study. Collectively, these results suggest that continuous red or blue + red light during the entire growth period can facilitate tomato fruit ripening, whereas light treatment only during the reproductive growth stage can delay fruit ripening compared to full-spectrum white light. Furthermore, red light or a mixture of blue and red light can induce higher levels of ethylene production and respiration rate, promoting fruit ripening [8,21,29]. Further physiological and molecular studies are necessary to reveal the underlying mechanisms of delayed fruit ripening resulting from red light irradiance during the reproductive stage.

As shown in Figure 4, at 82 DAA, the number of fruits that developed under red or blue + red light conditions was comparable to that under white light conditions. However, it was significantly lower in the blue-light-treated group. The number of immature and mature fruits in plants under blue light conditions was reduced by 35% and 16%, respectively, compared with those under white light (Figure 4A,B). Furthermore, the number of fruits was positively correlated with the number of flowers. Generally, blue light acts as a signal that promotes flowering not only in tomatoes but also in *Arabidopsis* [30–32], and which can increase the number of flowers by up to four times in a wide variety of plants, such as tulips [33], saffron [34], basil, and sweet pepper [35]. In contrast to previous studies, the observations in the present study suggest that applying 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue light instead of white or red light during the reproductive stage can negatively affect the fruit setting in tomatoes. This phenomenon was also observed under a mixture of blue and red light (1:1 ratio). The number of immature and mature fruits that developed under blue + red light conditions was between the observed values in the blue- and red-light treatment groups (Figure 4A,B).

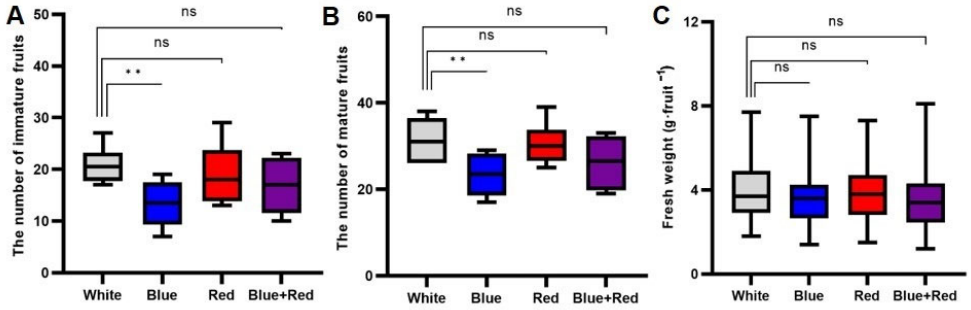


Figure 4. Effect of different light treatments during the reproductive stage on tomato fruit yield. (**A**,**B**) The number of immature and mature fruits in a plant determined at 82 days after anthesis in each light treatment group. (**C**) Fresh weight of a red-ripe stage fruit for each light treatment group. The square box means the value from the lower quartile of 25% (Q1) to the upper quartile of 75% (Q3) of the inter-quartile range (IQR), and the line inside the box is the median (50%). The upper and lower whisker lines outside the box represent the maximum and minimum values. *t*-tests were performed for each light treatment group (blue, red, or blue + red) against the white light treatment group (n = 6). Symbols denote statistical significance (n.s. = not significant; ** = $p < 0.01$).

Compared with white light, blue, red, or blue + red light irradiance during the reproductive growth stage did not appear to influence the fresh weight of fully mature tomato fruit (Figure 4C). However, the total fruit yield in a plant was reduced in the blue light treatment group, owing to the lower number of fruits produced in this group.

3.2. The Nutritional Characteristics of Tomato Fruits Developed and Matured under Different Light Conditions

Acidity and soluble sugars are recognized as primary components that contribute to the characteristic flavor of tomato fruits [36]. In general, the acidity of fully mature tomato fruit ranges from pH 3.6 to 4.2 [36]. The acidity of tomato fruit could be modulated by light conditions. As shown in Figure 5A, RR-stage tomato fruits harvested at 82 DAA

displayed reduced pH when grown under monochromatic blue, red, or their dichromatic light conditions compared to the multispectral white light treatment condition.

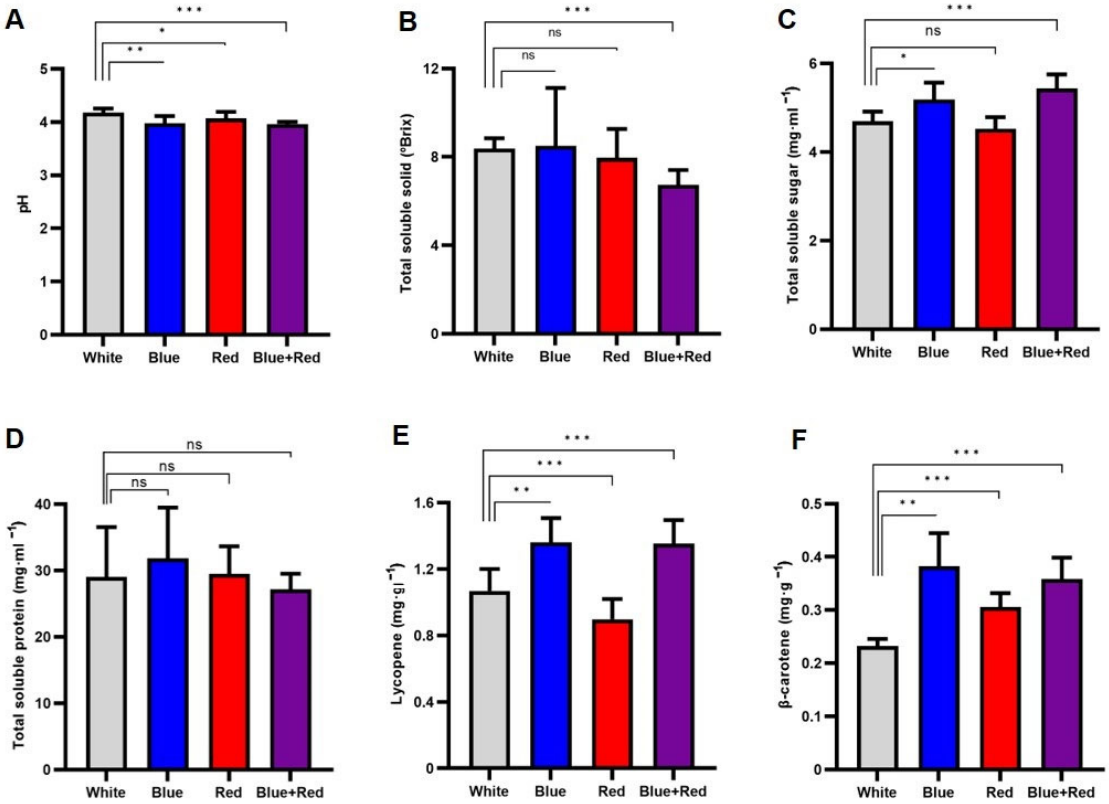


Figure 5. The nutritional characteristics of tomato fruits developed and matured under different light irradiance conditions. Tomato fruits in the red-ripe stage were harvested at 82 days after anthesis from each light treatment group. (**A**) pH. (**B**) Total soluble sugar content. (**C**) Total soluble solid content. (**D**) Total soluble protein content. (**E**) Lycopene content. (**F**) β-carotene content. Data are presented as mean (n = 6), and error bars indicate standard deviation. T-tests were performed for each light treatment group (blue, red, or blue + red) against white light treatment group. Symbols denote statistical significance (n.s. = not significant, * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

The total soluble sugar content was also affected by light conditions. It was 1.10 and 1.15 times higher under blue and blue + red light, respectively, than under white light conditions, while it remained unchanged under monochromatic red light conditions (Figure 5B). Similar to our study, previous studies have explored the effects of blue or blue + red light on the accumulation of soluble sugars in tomato fruits. The accumulation was higher under blue and red light in a 1:1 ratio than under monochromatic blue light conditions [37]. Furthermore, among the different ratios of blue and red light treatment groups, the group with a 3:2 ratio showed the highest soluble sugar content, with decreasing levels observed in the following order: 1:1, 1:3, and 3:1 ratios [37]. Compared with white light, a 1:3 ratio of blue and red light also induced the accumulation of glucose, fructose, and sucrose at higher levels [38]. In addition, this blue and red light mixture promoted the expression of enzymes such as beta-glucosidase, xylose isomerase, and 6-Phosphofructokinase 1, which are associated with soluble sugar accumulation in tomato fruits [38].

Although the blue + red light condition increased the total soluble sugar content in RR stage tomato fruit (Figure 5B), the content of total soluble solids was reduced in this light condition compared to white light (Figure 5C). This phenomenon suggests that blue + red light might reduce other nutritional components, such as organic acids and minerals, while increasing the sugar content in fully mature tomato fruits.

The total soluble protein content in RR-stage fruits grown under blue, red, or blue + red light conditions was comparable with that under the multispectral white light condition (Figure 5D), indicating that the accumulation of soluble protein would be unaffected by differences in the light spectra during fruit growth.

Lycopene and β-carotene are the most abundant carotenoids in tomato, and play important roles in various physiological processes including photosynthesis, pollination, and a/biotic stress responses in plants [39]. Furthermore, lycopene and β-carotene are essential components of human diets and well-known health-promoting phytochemicals with potent antioxidant activities [40]. The enhanced accumulation of these compounds could be directly associated with increased nutritional value as well as with the market value of tomatoes.

Tomato fruits that developed and matured under blue or blue + red light conditions had significantly higher amounts of lycopene and β-carotene than those that matured under white light conditions (Figure 5E,F). In particular, monochromatic blue light irradiation after anthesis increased the lycopene and β-carotene content by 27.1% and 65.2%, respectively, in tomato fruits at the RR stage compared to white light irradiation. Similar to the present results, monochromatic blue light and a mixture of blue and red light supplementation increased lycopene and β-carotene content during fruit maturation [7,12]. In natural and artificial light environments, blue light plays a key role in regulating various secondary metabolic processes, including carotenoid biosynthesis [41]. It stimulates the expression of photoreceptors, cryptochromes (CRYs), which inhibit the expression of transcription factors, phytochrome-interacting factors (PIFs), and elongated hypocotyl 5 (HY5). These transcription factors negatively regulate phytoene synthase (PSY), a key enzyme involved in carotenoid biosynthesis. Consequently, blue light induces the expression of PSY, thereby increasing the content of carotenoids such as lycopene and β-carotene [28,42–44].

Monochromatic red-light irradiance during the reproductive stages reduced the lycopene content by 16% but increased the β-carotene content by 32% compared to white light conditions. Unlike blue light, a monochromatic red light appeared to have no direct effect on stimulating carotenoid biosynthesis [42,43] but rather reduced the total polyphenol content and total flavonoid concentration, leading to rapid entry into the senescence stage [44].

4. Conclusions

Under the same light intensity conditions, when compared to multispectral light, monochromatic blue or red light, as well as their dichromatic mixture, could have varying impacts on tomato fruit development and nutrient accumulation during the reproductive growth stage. Red light or a mixture of blue and red light significantly delayed the ripening of the tomato fruit, whereas blue light did not alter the fruit ripening pace. Although the average weight per fruit remained unaffected by differences in light quality, the application of blue light reduced the number of fruits per plant. This study also demonstrated that blue light plays a crucial role in enhancing the nutritional value of tomato fruit, leading to elevated levels of soluble sugars, lycopene, and β-carotene. By amalgamating our findings with outcomes from earlier research, a more intricate light intervention strategy could be formulated to effectively regulate fruit maturation, ripening, and nutritional composition, while further research is needed to explore the physiological mechanisms underlying these trait changes induced by light.

Author Contributions: Conceptualization, S.H.L. and J.H.J.; methodology, S.H.L. and J.H.J.; software, S.H.L. and S.B.; validation, S.H.L., S.B. and J.H.J.; formal analysis, S.H.L. and H.J.W.; investigation, H.J.W. and H.C.; resources, H.C.; data curation, S.H.L. and H.J.W.; writing—original draft preparation, S.H.L., H.J.W. and J.H.J.; writing—review and editing, S.H.L., H.J.W. and J.H.J.; visualization, S.H.L.; supervision, J.H.J.; project administration, J.H.J.; funding acquisition, J.H.J. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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Conflicts of Interest: The authors declare no conflict of interest.

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