

## Article

# Growth Stage Specific Lighting Spectra Affect Photosynthetic Performance, Growth and Mineral Element Contents in Tomato

Giedrė Samuolienė , Jurga Miliauskienė, Algirdas Kazlauskas and Akvilė Viršilė \* 

Institute of Horticulture, Lithuanian Research Centre for Agriculture and Forestry, Kaunas str. 30, 54333 Babtai, Lithuania; giedre.samuoliene@lammc.lt (G.S.); jurga.miliauskiene@lammc.lt (J.M.); algirdas.kazlauskas@lammc.lt (A.K.)

\* Correspondence: akvile.virsile@lammc.lt

**Abstract:** The aim of study was to evaluate if the alternation in growth stage-specific lighting spectrum would be superior for tomato growth, photosynthesis, and mineral element contents compared to constant spectrum lighting. Dwarf tomato (*Solanum lycopersicum* L. cv. Micro Tom) was cultivated in controlled environment chamber (23/19 °C) under light emitting diode lighting. Three lighting spectrum treatments were set, optimized for different tomato growth stages: “seedling” (S; blue (B, 447 nm), red (R, 660 nm) and far red (FR, 740 nm) light), “growth” (G; R, B and FR light, supplemented with 523 nm green) and fruiting (F; R, B, FR light supplemented with 385 nm ultraviolet A (UV-A)). The total photon flux density of 250  $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$  was maintained in all treatments. Three lighting spectrums were alternated in seedling (S, G, F), biomass growth (SS, SG, GG, FF) and fruiting (SSS, SGG, GGG, GGF, FFF, SGF) stages of tomato creating growth stage-specific or constant lighting spectrum strategies. The light effects depended on tomato age, however the alternation in growth stage-specific lighting spectrum did not have a pronounced impact on dwarf tomato photosynthetic indices, growth, yield and mineral element content. The investigated parameters mainly depended on the spectrum of the latter growth stage.

**Keywords:** *Solanum lycopersicum*; lighting spectra; crop modeling; growths stages; photosynthesis; macroelements; microelements



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## 1. Introduction

Among light sources used in controlled environment agriculture (CEA), light-emitting diodes (LEDs) can be distinguished due to the possibility to tailor the light spectral composition and dosage of each spectral component. However, in CEA, seeking maximal vegetable productivity and external quality, often this deviates from natural plant needs. This leads to disturbed homeostasis and evokes early senescence processes, therefore plant nutritional quality, productivity is diminished, and the growth and development balance is violated. The customized, species-specific light spectrum allows us to modulate plant structural or physiological changes, therefore optimizing production and improving energy utilization efficiency [1–4].

Previously, the impacts of various light parameters on the photosynthesis process were analyzed: photosynthetically active radiation (PAR) intensity [5], light spectrum, including red to far-red light ratio [6], blue and red light ratio [7], combinations of blue and green light [8,9], as well as supplemental ultraviolet (UV)-A [10–12] and UV-B [13] radiation. To detect and to respond to light from UV-A to far red regions, plants absorb radiation through light-harvesting pigments and use a network of signaling components and transcriptional effectors [14,15]. Photosynthetic processes are regulated by light intensity and different light wavelengths, tailoring photochemical reaction efficiency, influencing the stomatal, chloroplast development, leaf pigment content, production and metabolism of primary and secondary metabolites [16].

Tomato is often used as a model plant for scientific purposes and is the most cultivated vegetable worldwide [17]. It is usually grown in greenhouses, however, in recent years, cases of tomato cultivation in closed controlled environments have also been rising [18–20]. Long-term cultivation to harvest tomatoes in plant factories is challenging, especially due to the lighting requirements. Most of the studies are limited to tomato seedling cultivation in CEA [21], as normal tomato yielding in CEA requires multicomponent lighting spectrum and remarkably higher photosynthetic photon flux density (PPFD). Tomato seedlings should be compact, well-rooted with a high leaf mass area and solid stems [17]. These quality attributes of plant seedlings are important for future growth and productivity in the greenhouse and can be obtained under well-proportioned red and blue light spectra [21,22]. After seedling establishment, rapid leaf expansion is desirable to increase light capture, create biomass and promote flowering initiation and initial fruit formation. Partially replacing a red and blue spectrum by green, results in increased biomass, specific leaf area, stem biomass, and length [23]. Finally, fruit ripening can be promoted, and phytochemical concentration increased by higher blue to red light ratio or supplemental UV-A light [24]. This proposes the idea of dynamic light manipulation by changing light recipes throughout the growth cycle [25]. Following that, we hypothesize, that combining several “fixed” spectrums during different tomato growth stages might result in superior photosynthesis, growth and mineral nutrition parameters. Therefore, the aim of our study was to evaluate the effects of the alternation of growth stage-specific lighting spectrum on dwarf tomato growth, photosynthesis and mineral element contents compared to constant spectrum lighting.

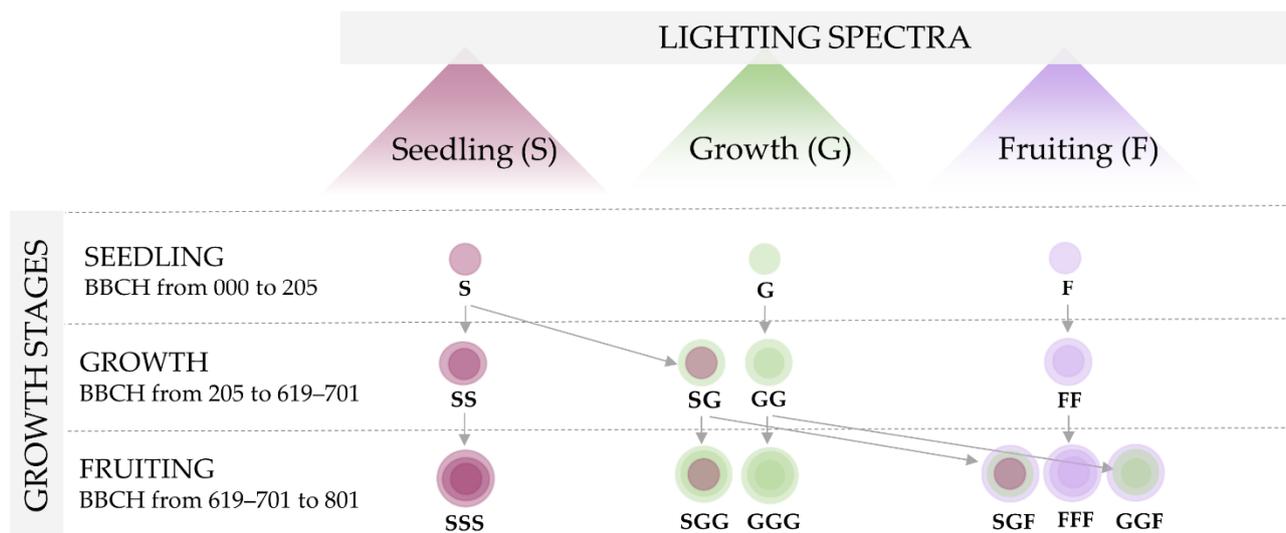
## 2. Materials and Methods

Tomato (*Solanum lycopersicum* L. cv. Micro Tom, dwarf, determinate type) were cultivated in a walk-in controlled-environment growth chamber (4 × 6 m, h = 3.2 m). Day/night temperatures of  $23 \pm 2/19 \pm 2$  °C within 16 h photoperiod and relative humidity of 60–70% and CO<sub>2</sub> level of ~700 ppm was maintained. Seeds were seeded into seedling trays, in the mixture (1:5) of perlite and peat substrate (Profi 1, JSC Durpeta, Lithuania) (pH 6). The average amounts of nutrients (mg·L<sup>-1</sup>) in the substrate were N, 110; P<sub>2</sub>O<sub>5</sub>, 50; K<sub>2</sub>O, 160, supplemented with microelements Fe, Mn, Cu, B, Mo and Zn. Electrical conductivity of substrate (EC) varied between 2.0 and 2.5 mS/cm ( $\pm 0.03$  mS/cm). In the seedling stage (205–206 according to the BBCH (Biologische Bundesanstalt, Bundessortenamt and Chemical Industry) scale) tomatoes were transplanted into plastic vessels (110 × 110 mm, h = 120 mm) with peat substrate (Profi1, Durpeta, Lithuania)-one plant per vessel; 20 vessels for each lighting treatment replication (60 vessels per treatment). Plants were watered maintaining equal substrate humidity. Seedlings on the 3rd week from germination were fertilized with NPK 3-1-3 liquid fertilizers (Plagron, Netherlands; 66, 22 and 66 mg·L<sup>-1</sup> of N, P and K respectively) and, after transplanting, fertilized with NPK 2-2-4 liquid fertilizers (Plagron, Netherlands; 44, 44 and 88 mg·L<sup>-1</sup> of N, P and K), twice a week.

Controllable lighting fixtures (HLRD, Hortiled, Lithuania), consisting of red (660 nm), blue (447 nm), far red (740 nm), green (523 nm) and UV-A (385 nm) light-emitting diodes (LED) were used for illumination. Three different lighting spectrum treatments (three replications (individual fixtures) per lighting spectrum treatment) were set, each optimized according to previous experimental experience for different tomato growth stages: seedling, growth, and fruiting [26] (Table 1, Figure 1). Lighting fixtures were arranged randomly in the growth chamber and separated with light-proof fabric partitions. The total photon flux density (PPFD) of 250  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (total daily light integral, DLI = 14.40  $\text{mol}\cdot\text{m}^{-2}\cdot\text{per}\cdot\text{day}$ ) was maintained in all treatments. “Seedling” lighting spectrum consisted of red and blue LED wavelengths (30% of blue), supplemented with low PPFD of far red light. In the “growth” stage lighting spectrum, 10% of blue light was replaced with green for higher photosynthetic productivity, when in fruiting growth stage, red, blue and far red LED components were supplemented with 1.6  $\text{mW}\cdot\text{cm}^{-2}\cdot\text{UV-A}$  light.

**Table 1.** Experimental lighting spectra. Photon flux densities (PFD) of individual spectrum components.

Lighting Spectra	Blue 447 nm $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Red 660 nm $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Far Red 740 nm $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Green 523 nm $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	UV-A 385 nm $\text{mW}\cdot\text{cm}^{-2}$
Seedling (S)	75	165	10	-	-
Growth (G)	50	165	10	25	-
Fruiting (F)	60	180	10	-	1.6

**Figure 1.** Experimental lighting design.

PFD was measured and regulated at the vessel level using a photometer–radiometer (RF-100, Sonopan, Białystok, Poland). Irradiance level from UV LEDs measured with calibrated spectrometer (Ocean Optics Flame-S-UV-VIS-ES, Orlando, FL, USA) with a cosine corrector (Ocean Optics CC-3-DA, Orlando, FL, USA).

For each tomato growth stage (Figure 1), plants were shifted between lighting treatments. In the initial growth stage (BBCH 000–205), the impact of “seedling” (S), “growth” (G) and “fruiting” (F) spectra on tomato growth and photosynthesis parameters were compared. In the stage of tomato growth and biomass accumulation, until the emergence of initial inflorescences (from 3rd to 8th week after germination; BBCH from 205 to 619–701), plants were further cultivated under the same spectrum (SS, GG, FF), but part of the plants were moved from the “seedling” to “growth” spectrum (SG). From BBCH 619–701 to 801 (ripening of first fruits; 8th to 12th week after germination), plants were cultivated under the same spectrum (SSS, GGG, FFF and SGG) and part of the plants from the “growth” spectrum were shifted to the “fruiting” spectrum (SGF, GGF), seeking to create growth-stage specific alteration of lighting spectrum and compare to the response of tomato plants cultivated under constant lighting spectrum.

Plant growth and photosynthetic response were evaluated at the end of each growth stage/lighting treatment. At the end of the growth stage, mineral element contents were evaluated in tomato leaves. All parameters were evaluated in three experimental and three analytical replications.

Leaf gas exchange indices: photosynthesis rate ( $P_r$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$ ), transpiration rate ( $T_r$ ,  $\text{mmol}\cdot\text{H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), stomatal conductance ( $g_s$ ,  $\text{mol}\cdot\text{H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), water usage efficiency (WUE,  $\mu\text{mol}\cdot\text{CO}_2\cdot\text{mmol}^{-1}\cdot\text{H}_2\text{O}$ ) and light usage efficiency (LUE,  $\text{mol}\cdot\text{CO}_2\cdot\text{mol}^{-1}\cdot\text{photons}$ ) were measured on the third developed leaf, using a portable photosynthesis system (LI-COR 6400XT, Lincoln, NE, USA) under the leaf chamber conditions of 21 °C, with a  $\text{CO}_2$  concentration of 400  $\mu\text{mol}\cdot\text{mol}^{-1}$  and 60% relative humidity, PPFD 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Measurements were performed from 9 to 12 a.m.

Chlorophyll fluorescence was measured using red (660 nm) and blue (450 nm) excitation wavelengths as measuring light, using multi-mode chlorophyll fluorometer acquisition system (OS5p, Opti-Sciences, Hudson, NH, USA). Measurements of light-adapted steady state chlorophyll fluorescence ( $F'$ ), light-saturated chlorophyll fluorescence ( $F'_m$ ), and  $F'_0$  were used to calculate the relative PSII (photosystem II) operating efficiency ( $\Phi_{PSII}$ ). Dark-adapted (40 min)  $F_0$  and  $F_m$  measurement allowed the calculation of the maximum quantum efficiency of PSII ( $F_v/F_m$ ).

Spectral reflectance was measured using a leaf spectrometer (CID Bio-Science, Camas, WA, USA) from 9 to 12 a.m. Reflection spectra registered was used to calculate photochemical reflectance index (PRI), which shows changes in the xanthophyll cycle, using the following formula:

$$PRI = \rho_{531} - \rho_{570} / \rho_{531} + \rho_{570} \quad (1)$$

where  $\rho_{531}$  and  $\rho_{570}$  represent the leaf reflectance integrated over a 10 nm wavelength band centered on 531 and 570 nm, respectively.

**Elemental analysis.** For macro and micro element analysis 0.4 g (dry weight) of leaves was digested with 6 mL  $HNO_3$  and 2 mL  $H_2O_2$  in a microwave digestion system (Multiwave GO, AntonPaar, Austria). The resulting solutions were cooled and diluted to 50 mL with distilled water and analyzed by ICP-OES (Inductively coupled plasma - optical emission spectrometry; Spektro Genesis, SPECTRO Analytical Instruments GmbH, Kleve, Germany). The calibration curves for all the studied elements were in the range of 0.01 to 1.0  $mg \cdot L^{-1}$  [27]. Data are presented as  $mg \cdot g^{-1}$  in dry plant weight.

**Biometric measurements.** At the end of seedling and growth stages, plant fresh (FW) and dry (DW) weight and leaf area were evaluated. In the fruiting stage, tomato fruit weight and number per plant were evaluated. DW was weighed after tissue dehydration at 70 °C for 48 h (Venticell-BMT, Czech Republic). Leaf area (LA) was determined by using an automated leaf area meter (AT Delta-T Devices, Cambridge, UK).

**Statistical analysis.** The data were processed using MS Excel (version 7.0; Microsoft Inc., Redmond, WA, USA) and XLStat software (Addinsoft, 2019, New York, NY, USA). Analysis of variance (ANOVA) using Fisher's test at the confidence level  $p = 0.05$  and multivariate principal component analysis (PCA) were performed. The results are presented in the PCA scatterplot, which indicate distinct differences between photosynthetic indices in tomato leaves under the different lighting spectra during different growth stages.

### 3. Results

It was presumed, that growth stage-specific lighting spectrum conditions would be more favorable for plants, compared to constant lighting conditions during the whole growth cycle. The performed experiments explored the impacts of alternating lighting spectrum on tomato photosynthetic performance, growth, yield parameters and mineral element contents.

#### 3.1. Photosynthetic Performance

The lighting spectrum had a significant impact on tomato photosynthetic response (Table 2). In the initial growth stage (BBCH 000 to 205), the "seedling" (S) spectrum, consisting of red and blue and far red light resulted in 1.3 times and 1.2 times higher transpiration rate ( $Tr$ ) and stomatal conductance ( $gs$ ), but did not have significant impact on photosynthesis rate ( $Pr$ ), compared to the "growth" (G) spectrum. As a result, significantly lower water-use efficiency (WUE) was determined. The "fruiting" (F) light spectrum was not beneficial for the photosynthetic performance of young seedlings, as indicated by lower  $Pr$ , lower  $F_v/F_m$  and PRI. The response of dark-adapted photochemical reactions of PSII ( $F_v/F_m$  0.73) indicates that even low intensity of UV-A light in F spectrum causes photoinhibition in tomato seedlings; however, light adapted quantum photosynthetic yield of PSII was significantly higher (Table 2).

**Table 2.** Photosynthetic response of tomato subjected to different light spectrum during growth stages\*. Different letters indicate statistically significant differences between means according to Fisher’s test at the confidence level  $p = 0.05$ . S, G and F—lighting spectrum, selected for “seedling”, “growth” and “fruiting” stages, respectively, and alternated in seedling (S, G, F), biomass growth (SS, SG, GG, FF) and fruiting (SSS, SGG, GGG, GGF, FFF, SGF) tomato growth stages.

Treatment	Pr, $\mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$	Tr, $\text{mmol H}_2\text{O m}^{-2} \cdot \text{s}^{-1}$	gs, $\text{mol H}_2\text{O m}^{-2} \cdot \text{s}^{-1}$	WUE, $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$	LUE, $\text{mol CO}_2 \text{ mol}^{-1} \text{ Photons}$	F <sub>v</sub> /F <sub>m</sub>	$\Phi_{\text{PSII}}$	PRI
			Seedling: BBCH from 000 to 205					
S	23.6 <sup>a</sup>	4.50 <sup>a</sup>	0.82 <sup>a</sup>	31.4 <sup>b</sup>	0.019 <sup>a</sup>	0.81 <sup>a</sup>	0.75 <sup>b</sup>	0.08 <sup>ab</sup>
G	21.0 <sup>ab</sup>	3.56 <sup>b</sup>	0.51 <sup>b</sup>	43.1 <sup>a</sup>	0.017 <sup>ab</sup>	0.82 <sup>a</sup>	0.76 <sup>b</sup>	0.09 <sup>a</sup>
F	20.6 <sup>b</sup>	3.29 <sup>b</sup>	0.56 <sup>b</sup>	41.4 <sup>a</sup>	0.017 <sup>b</sup>	0.73 <sup>b</sup>	0.79 <sup>a</sup>	0.07 <sup>b</sup>
			Growth: BBCH from 205 to 619–701					
SS	16.6 <sup>a</sup>	2.57 <sup>a</sup>	0.11 <sup>a</sup>	155.8 <sup>a</sup>	0.07 <sup>a</sup>	0.83 <sup>a</sup>	0.77 <sup>b</sup>	0.08 <sup>b</sup>
SG	12.6 <sup>c</sup>	1.44 <sup>bc</sup>	0.06 <sup>bc</sup>	207.0 <sup>a</sup>	0.05 <sup>c</sup>	0.83 <sup>a</sup>	0.78 <sup>ab</sup>	0.08 <sup>b</sup>
GG	5.8 <sup>d</sup>	1.13 <sup>c</sup>	0.05 <sup>c</sup>	155.2 <sup>a</sup>	0.02 <sup>d</sup>	0.81 <sup>b</sup>	0.79 <sup>a</sup>	0.08 <sup>b</sup>
FF	14.6 <sup>b</sup>	1.78 <sup>b</sup>	0.08 <sup>b</sup>	196.3 <sup>a</sup>	0.06 <sup>b</sup>	0.83 <sup>a</sup>	0.78 <sup>ab</sup>	0.09 <sup>a</sup>
			Fruiting: BBCH from 619–701 to 801					
SSS	12.6 <sup>ab</sup>	1.81 <sup>a</sup>	0.05 <sup>a</sup>	233.4 <sup>c</sup>	0.05 <sup>ab</sup>	0.81 <sup>ab</sup>	0.08 <sup>a</sup>	0.08 <sup>a</sup>
SGG	10.6 <sup>b</sup>	1.08 <sup>b</sup>	0.04 <sup>ab</sup>	297.6 <sup>bc</sup>	0.04 <sup>b</sup>	0.81 <sup>ab</sup>	0.08 <sup>a</sup>	0.08 <sup>a</sup>
GGG	10.7 <sup>b</sup>	1.27 <sup>ab</sup>	0.04 <sup>ab</sup>	273.0 <sup>bc</sup>	0.04 <sup>b</sup>	0.81 <sup>ab</sup>	0.08 <sup>a</sup>	0.08 <sup>a</sup>
SGF	15.6 <sup>a</sup>	1.14 <sup>b</sup>	0.04 <sup>ab</sup>	427.4 <sup>ab</sup>	0.06 <sup>a</sup>	0.79 <sup>b</sup>	0.07 <sup>a</sup>	0.07 <sup>a</sup>
FFF	15.4 <sup>a</sup>	1.39 <sup>ab</sup>	0.05 <sup>a</sup>	323.9 <sup>bc</sup>	0.06 <sup>a</sup>	0.82 <sup>a</sup>	0.07 <sup>a</sup>	0.07 <sup>a</sup>
GGF	15.2 <sup>a</sup>	0.92 <sup>b</sup>	0.03 <sup>b</sup>	565.3 <sup>a</sup>	0.06 <sup>a</sup>	0.81 <sup>ab</sup>	0.07 <sup>a</sup>	0.07 <sup>a</sup>

\* Pr—photosynthesis rate, Tr—transpiration rate, gs—stomatal conductance, WUE—water usage efficiency, LUE—light usage efficiency, F<sub>v</sub>/F<sub>m</sub>—maximum quantum efficiency of PSII (photosystem II),  $\Phi_{\text{PSII}}$ —relative PSII operating efficiency, PRI—photochemical reflectance index. Different letters indicate statistically significant differences between means according to Fisher’s test at the confidence level  $p = 0.05$ .

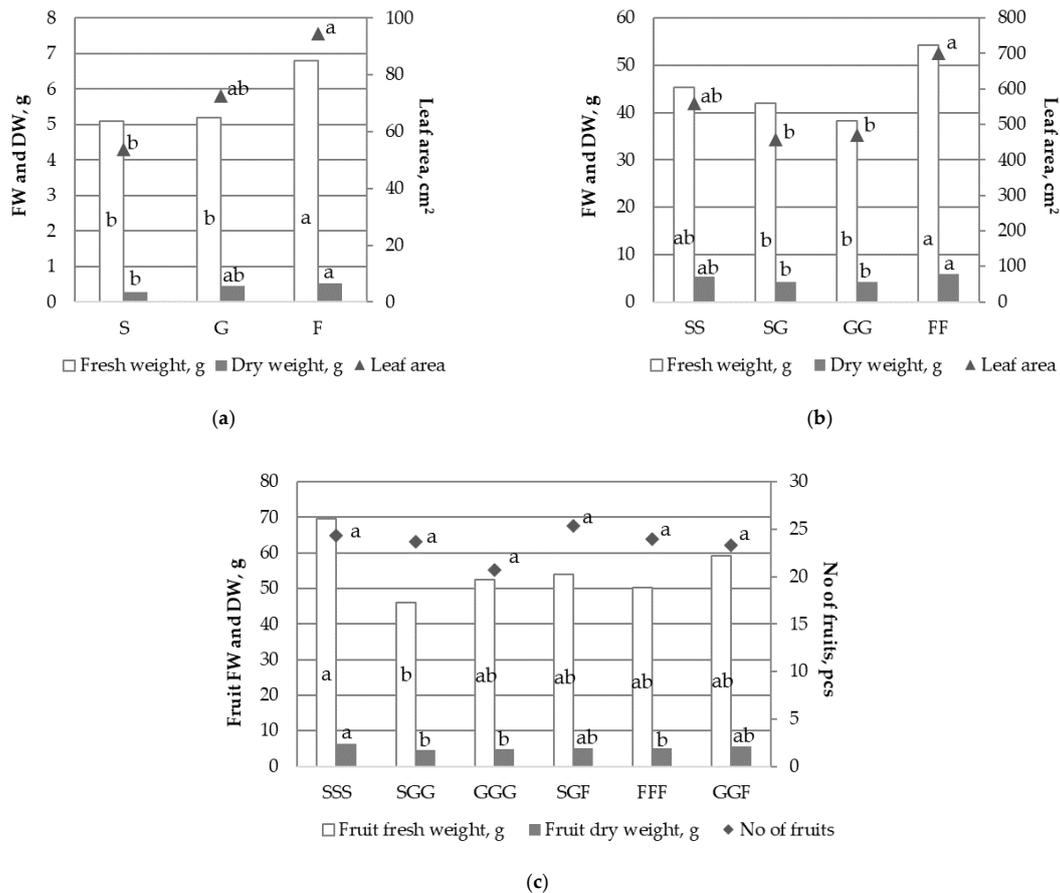
In the growth stage, BBCH 205 to 619–701, the photosynthetic responses to alternating lighting conditions were more pronounced. Pr, Tr and gs, similarly to the seedling stage, were the highest in tomato plants, illuminated with S spectrum during both growth stages (SS). Pr and Tr were determined 2.9 and 2.3 times higher compared to the plants under constant “growth” (GG) spectrum and 1.2 and 1.3 times higher than under alternating SG spectrum. The photosynthetic parameters of tomato plants, cultivated under FF spectrum were intermediate between SS and GG spectrum. Fluorescence parameters and PRI varied insignificantly in this growth stage.

For the fruiting growth stage (BBCH 619–701 to 801), plants were replaced between lighting spectrum repeatedly. Photosynthesis rate (Pr), as well as LUE and WUE were the highest in tomato plants in the fruiting stage under F spectrum, supplemented with UV-A light, however, no differences were observed between constant and alternating lighting spectrum exposure (SGF, FFF and GGF treatments). Meanwhile, SGF lighting spectrum exposure resulted in 1.5 times higher Pr, compared to SGG lighting.

Unlike other growth stages, during fruiting Tr was remarkably different from Pr. Tr was the highest in lighting treatments, where lighting spectrum was constant during all growth stages—SSS, GGG and FFF. The difference in fluorescence parameters were not remarkable, however, the alternating during growth stages light spectrum SGF resulted in lower F<sub>v</sub>/F<sub>m</sub> (Table 2).

### 3.2. Growth and Yield Parameters

Lighting spectrum in the seedling growth stage (Figure 2a) had a pronounced impact on tomato seedling biometric parameters. Notwithstanding to negative impact on Pr, F lighting spectrum, containing UV-A light, resulted in the highest tomato seedling fresh and dry weight and leaf area (1.3 times higher compared to S). During the biomass growth stage (Figure 2b), the “growth” spectrum, containing supplemental green light, slightly reduced leaf area and fresh plant weight, compared to SS and FF, however, no differences were obtained between constant GG and alternating SG spectrum. In the fruiting growth stage (Figure 2c), the changes in light spectrum had no impact on the number of fruits per plant, SSS lighting resulted in slightly higher biomass of fruits per plant.



**Figure 2.** Growth and yield parameters of tomato, illuminated with different light spectrum during growth stages: (a) plant growth parameters during seedling stage; (b) plant growth parameters during growth stage; (c) fruit yield obtained in fruiting stage. Different letters indicate statistically significant differences between means according to Fisher’s test at the confidence level  $p = 0.05$ . S, G and F—lighting spectrum, selected for “seedling”, “growth” and “fruiting” stages respectively and alternated in seedling (S, G, F), biomass growth (SS, SG, GG, FF) and fruiting (SSS, SGG, GGG, GGF, FFF, SGF) tomato growth stages.

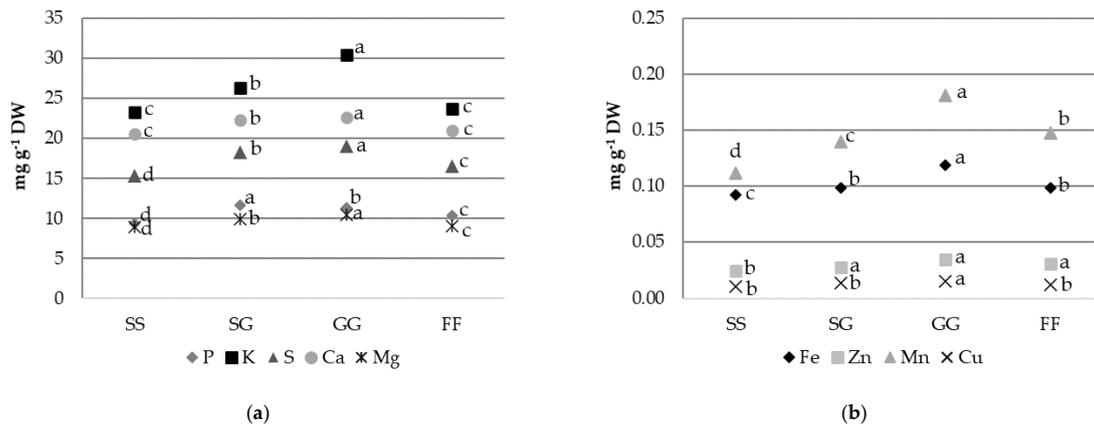
### 3.3. Mineral Element Contents

Mineral element contents in tomato leaves were evaluated in the growth stage (Figure 3). Similar variation was determined for all macro (Figure 2a) and micro (Figure 2b) elements. Green light in G spectrum resulted in the highest mineral accumulation in SG and GG illuminated plants. The contents of all minerals in the GG treatment, where tomato plants in seedling and growth stages were cultivated under green light, supplementing red and blue spectrum were 1.2–1.6 times higher, compared to SS. K and Mg variation were the most pronounced.

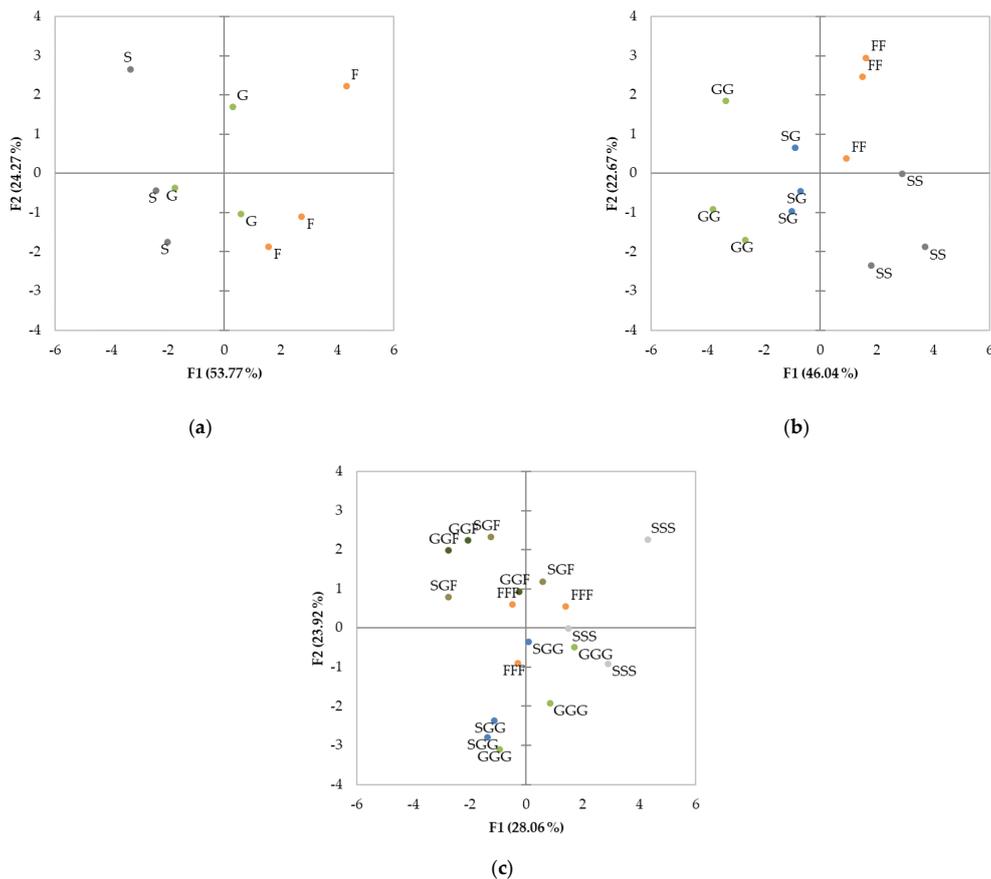
### 3.4. Principal Component Analysis

The results of principal component analysis (PCA) confirm, that differences between growth-stage specific lighting impacts on tomato growth and photosynthesis are subtle (Figure 4). The PCA results in seedling stage are scattered (Figure 4a), however S spectra impacts are more differentiated from G, than F spectra. In the growth stage (Figure 4b), constant spectrum treatments, SS, GG and FF, according to growth and photosynthetic indices significantly differ from each other, however, there are no significant difference between GG and SG treated tomato, which in this growth stage were cultivated under similar spectrum, but in the seedling stage lighting spectrum was different. In the fruiting stage (Figure 4c), in contrast to growth stage, constant lighting spectrum treatments (FFF,

SSS, FFF) did not differ from each other. Alternating lighting spectrum SGG did not differ from GGG; while GGF and SGF did not differ from FFF.



**Figure 3.** Mineral element contents in tomato leaves in the “growth” stage, illuminated with different light spectrums during growth stages: (a) macroelements; (b) microelements. Different letters indicate statistically significant differences between means according to Fisher’s test at the confidence level  $p = 0.05$ .



**Figure 4.** The PCA scatterplots, indicating distinct differences in photosynthetic performance of tomato, cultivated under different lighting spectrums during different growth stages: (a) seedling; (b) growth; (c) fruiting. S, G and F—lighting spectrum, selected for “seedling”, “growth” and “fruiting” stages respectively and alternated in seedling (S, G, F), biomass growth (SS, SG, GG, FF) and fruiting (SSS, SGG, GGG, GGF, FFF, SGF) tomato growth stages.

#### 4. Discussion

In natural habitats, plants are affected by changing light environment during their life cycle [16]: leaves are subjected to spatial and temporal gradients in incident light, which is the key resource for photosynthesis and plants acclimate to the light environment under which they are grown to maintain performance and fitness [28]. Therefore, it was expected that alternation in the lighting spectrum would be beneficial for plants and would enable us to tailor desirable morphological parameters and more efficient productivity (Figure 1). The results obtained confirm the modest impact of alternating the growth stage-specific lighting spectrum on Micro Tom tomato photosynthesis and growth.

In the seedling stage, the impact of different lighting spectrum on photosynthesis rate in young plants was not pronounced, as all investigated spectral combinations were efficient for photosynthesis. However, stomatal conductance and transpiration rates varied significantly, possibly due to wavelength specific control of stomatal function [29]. Red, far red and blue light combination in the “seedling” (S) light spectrum was efficient for acceptable tomato seedling growth and photosynthesis parameters [21,30]. Due to high photosynthetic and photon efficacy [31,32], red and blue light make the background of horticultural LED lighting, while a small flux of far red light is known to be beneficial for tomato growth, development and morphology [33]. However, the addition of the small flux of UV-A light in “fruiting” (F) spectra resulted in 1.2–1.3 times higher seedling dry weight and leaf area. Slightly lower  $P_r$ , but also decreased value of  $F_v/F_m$  (0.73) indicate possible mild photostress conditions under supplemental UV lighting in young plants, but no negative longer-term impacts on photosynthesis or growth were determined. Zhang et al., 2020 [24], analyzing impacts of supplemental UV-A on tomato plants concluded, that UV-A cannot be unequivocally considered as an abiotic stress factor and it functions similarly to blue light in maintaining leaf photosynthetic functioning [24]. However, in our study, UV-A enriched lighting treatment significantly differs from blue and red light impact on young tomato Micro Tom seedlings (Figure 4a).

In the growth stage, the impact of current lighting spectrum on tomato growth and photosynthetic performance was significant (Figure 4b), however, contrary to our expectations, no significant impact was obtained from the changes in lighting spectrum during seedling and growth stages (SG compared to GG). The highest photosynthesis indices,  $P_r$ ,  $T_r$  and  $g_s$  were determined in tomato, cultivated under S lighting spectrum during both growth stages (SS). Green light enriched the spectrum, and GG resulted in slightly lower tomato leaf biomass. Moreover, variation in growth stage-specific lighting spectrum (SG compared to GG) resulted in 1.2–1.3 lower photosynthetic indices. Kaiser et al., 2019 [23] reported that in greenhouse experiments partially replacing a red:blue spectrum by green increased tomato leaf mass by up to 6.5%, as well as specific leaf area, stem biomass and length. Although per unit leaf area, green light drives photosynthesis less efficiently than does red light, on a whole-plant level green light may increase growth due to changes in vertical light distribution, leaf light acclimation and canopy architecture [23]. However, in this study, experiments were performed in controlled environment growth chambers, where natural lighting background was eliminated. Moreover, the choice of plant growth stage for light spectrum experiments could have great effect on plant response [25].

Despite the insignificant or slightly inhibiting impact of green light on tomato growth and photosynthesis, it had remarkable impact on micro and macro element contents in leaves. In the growth stage, we determined 1.2–1.6 times higher P, K, S, Ca, Mg as well as Fe, Mn, Zn and Cu in tomato illuminated with the GG spectrum, with the highest variation of potassium and magnesium. The alternating growth stage-specific SG spectrum had a lesser impact on mineral element accumulation in tomato, but still slightly higher, than in SS and comparable to FF treated tomato. Previous studies also confirm that light spectral manipulations might be potent for the regulation of mineral element contents in plants [34–36].

The analysis of results obtained in the fruiting stage proposes (Figure 4c) that all investigated light spectrum combinations were favorable for the ‘Micro Tom’ dwarf tomato

growth and photosynthesis. However, the measured parameters were mostly affected by the lighting conditions in the latter growth stage. The lighting history—the enduring value of the lighting in the previous growth stage—was eliminated. SGF lighting treatment, where the lighting spectrum was changed at each growth stage resulted in ~1.5 times higher photosynthesis rate in the fruiting stage but, according to overall yield and photosynthetic indices alternating the lighting spectrum was not significant: SGG did not differ from GGG, while GGF = SGF = FFF. Photosynthesis rate, together with LUE and WUE were determined higher in plants, which were illuminated with a UV-A enriched F spectrum, however, upon general evaluation, there are no differences between FFF, GGG and SSS treatments.

## 5. Conclusions

Light spectrum effects are tomato age-specific, however the alternation in growth stage-specific lighting spectrum under selected experimental conditions did not have pronounced impact on dwarf tomato ‘Micro Tom’ photosynthetic indices, growth, yield and mineral nutrition parameters in CEA. The investigated parameters mainly depended on the spectrum of the latter growth stage. Despite the minor impact on growth and photosynthesis parameters, the impact of the alternating, growth stage-specific light spectrum on other tomato genotypes and on primary and secondary tomato metabolism, seeking production quality is worth exploring.

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