ORIGINAL ARTICLE

Light spectrum affects growth, metabolite profile, and resistance against fungal phytopathogens of *Solanum lycopersicum* L. seedlings

Alicja Tymoszuk[1]*◉, Dariusz Kulus[1]◉, Jolanta Kowalska[2]◉, Alicja Kulpińska[1], Dariusz Pańka[3]◉, Małgorzata Jeske[3]◉, Małgorzata Antkowiak[2]◉

[1] Laboratory of Horticulture, Faculty of Agriculture and Biotechnology, Bydgoszcz University of Science and Technology, 85-029 Bydgoszcz, Poland

[2] Department of Organic Agriculture and Environmental Protection, Institute of Plant Protection – National Research Institute, 60-318 Poznań, Poland

[3] Department of Biology and Plant Protection, Faculty of Agriculture and Biotechnology, Bydgoszcz University of Science and Technology, 85-796 Bydgoszcz, Poland

Abstract

Tomato is a widely cultivated and economically important crop worldwide. This study aimed to test the effect of light spectra used in indoor cultivation on the growth, biochemical profile, and resistance of *Solanum lycopersicum* 'Bawole Serce' seedlings against *Alternaria alternata*, *Alternaria solani* and *Botrytis cinerea*. During the phase of first leaf emergence, the seedlings were transferred to a semi-sterile growth room with a controlled environment (20°C, 18-h photoperiod, 50 µmol · m^{-2} · s^{-1} PPFD, 65% RH) for a 3-week cultivation period. Five light treatments differing in red/blue (R/B) light ratio were tested: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20). The best parameters in terms of shoot length, shoot fresh and dry weights, and number of leaves were obtained in treatment I, in contrast to IV and V. Plants from treatments IV and V had the smallest leaf area, perimeter, vertical length, and horizontal width. As for the root system, the highest fresh weight, area, length of the longest root, total length, and the number of root tips and forks were found in treatments I and II. The least developed root systems were observed in IV and V. The greatest chlorophyll, carotenoids and anthocyanins accumulation was enhanced by treatment II. Treatments I−III stimulated the biosynthesis of phenolic compounds. The highest superoxide dismutase activity was detected in plants from treatments I and II. As for *A. alternata* and *A. solani*, the level of disease symptoms was significantly higher for treatments IV and V than for I-III. The highest/lowest level of *B. cinerea* infection was found in treatments II/I, respectively. The least susceptible to infection by all tested pathogens were leaves from treatment I. Light spectrum composition is of practical importance for tomato seedling production.

Keywords: LED light, plant disease, plant metabolites, plant morphology, tomato cultivation

Introduction

Tomato (*Solanum lycopersicum* L.) is a broadly cultivated fruit belonging to the Solanaceae family. It is a crop of economic importance and one of the top vegetables consumed worldwide (Abdeldym *et al.* 2020). Global tomato production reached 180,766,329 million tons in 2019 (El-Mansy *et al.* 2021). The

nutritional composition of tomato fruit is rich in various biologically active compounds. Notable groups include carotenoids, such as lycopene, which is associated with antioxidant properties and has been linked to potential health benefits, particularly in cardiovascular health and cancer prevention (Mazidi *et al.* 2020). Additionally, tomatoes contain flavonoids, such as quercetin and kaempferol, known for their antioxidant and anti-inflammatory properties (Raiola *et al.* 2014; Cuevas-Cianca *et al.* 2023). Vitamin C, another essential component, contributes to immune function and collagen synthesis (DePhillipo *et al.* 2018).

Over the years, the demand for high-quality tomatoes has led to the development and implementation of controlled cultivation methods in greenhouses, growth rooms or vertical farms with regulated environments – the so-called controlled environment agriculture (CEA) (Dsouza *et al.* 2023). These indoor methods aim to optimize growth conditions, improve crop productivity, and enhance fruit quality through the precise manipulation of various environmental factors, including temperature, humidity, light, carbon dioxide (CO_2) level, and nutrient availability (Sotelo-Cardona *et al.* 2021). By carefully managing these parameters, growers can manipulate plant growth and development, optimize photosynthesis and fruit set, and regulate plant health (Amirahmadi *et al.* 2023). Controlled cultivation methods offer numerous benefits, including improved crop quality, year-round production, reduced water usage, and minimized reliance on agrochemicals. Additionally, CEA methods can help to develop methods of combating pathogens that pose a threat to the cultivation of tomato (Meiramkulova *et al.* 2021).

Light is a crucial factor that profoundly influences the growth and development of plants. Through photosynthesis, plants harness light energy to convert CO_2 and water into glucose and oxygen, fueling their growth and providing the foundation of most terrestrial ecosystems (Nguyen *et al.* 2021). In addition to photosynthesis, light plays a significant role in various physiological processes, including seed germination, photomorphogenesis, photoperiodism, and flowering. Moreover, it can influence the production of secondary metabolites, such as sugars, flavonoids, and aromatic substances in plants; thus, it can be used for the production of vegetables with increased levels of antioxidant compounds (Wang *et al.* 2022). These compounds not only contribute to the nutritional value of crops but also are involved in protecting against oxidative stress and certain chronic diseases, including cardiovascular disease, cancers, and age-related macular degeneration (Mazidi *et al.* 2020). Therefore, the intensity, duration, and spectral composition of light can affect the enzymatic and non-enzymatic defense mechanisms in plants, ultimately impacting their health and resistance to pathogens. Light has been shown to influence the susceptibility of vegetable plants to various bacterial (*Leuconostoc mesenteroides*) and fungal (*Botrytis cinerea*, *Fusarium graminearum* and *Penicillium digitatum*) pathogens (De Lucca *et al.* 2012; Rasiukevičiūtė *et al.* 2021). For instance, UV-B radiation can induce the production of flavonoids and phenolic compounds in lettuce, which have antimicrobial properties (Liu *et al.* 2023). Furthermore, light quality and intensity can affect the expression of defense genes, such as those encoding pathogenesis-related proteins and enzymes participating in the synthesis of phytoalexins (Escobar-Bravo *et al.* 2019). Understanding the interactions between light and disease resistance mechanisms can provide insights into developing sustainable strategies for disease control in tomato cultivation.

The availability and spectral composition of light in the growing environment can be manipulated using various lighting technologies, such as light-emitting diodes (LEDs), enabling precise control over plant growth and physiology (Fylladitakis *et al.* 2023). LEDs have several beneficial properties compared to formerly used lamp types, e.g. fluorescent tubes (FL). Among them are their low energy consumption and radiant heat output, rapid response time, long duration, and the availability of precise control of narrowband-emitting diodes (Proietti *et al.* 2021). Presumably, this latter characteristic allows for the scheduled induction of physiological responses of plants based on the light spectrum, ensuring the development of suitable defense systems against fungal pathogens of tomato.

Among some of the most common pathogens found in tomato, one can mention *Alternaria alternata* and *Alternaria solani* – the cause of early blight and *Botrytis cinerea* – the causal agent of gray mold. These three fungal pathogens can severely affect tomato plants, leading to significant yield losses and reduced fruit quality (Adhikari *et al.* 2017; Soltis *et al.* 2019). Understanding the role of light in the management of *A. alternata*, *A. solani* and *B cinerea* opens up possibilities for light-based disease management strategies in tomato cultivation. By utilizing specific light wavelengths and intensities, growers can create an unfavorable environment for fungal growth and infection. However, to date, only the effect of monochromatic LED lights (blue, red and far-red) on the resistance to gray mold in tomato has been studied (Kim *et al.* 2013 ; Courbier *et al.* 2021).

This study aimed to test the effect of five light treatments differing in the share of ultraviolet, blue, green, red and far-red light in their spectral composition on the shoot and root system growth, metabolite profile (content of chlorophylls, carotenoids, anthocyanins and phenolic compounds), and resistance of *S. lycopersicum* 'Bawole Serce' seedlings against *A. alternata*, *A. solani* and *B. cinerea*. This knowledge will contribute

to the advancement of tomato seedling production and the development of more targeted and sustainable disease management strategies against *A. alternata*, *A. solani*, and *B. cinerea* infections.

Materials and Methods

Plant material, cultivation, light treatment

Seeds of tomato (*Solanum lycopersicum* L.) 'Bawole Serce' were bought at PlantiCo Ltd. (Zielonki Parcela, Poland). On March 22, 2023, the seeds were surface disinfected before sowing. After rinsing under running tap water, the seeds underwent a series of treatments, including immersion in a 5% (*v/v*) detergent solution for 10 min, a 70% (*v/v*) ethanol solution for 5 min, and a 1.5% (*v/v*) NaClO solution for 20 min (all chemicals were supplied by Chemia Sp. z o.o., Bydgoszcz, Poland). Afterward, the seeds were rinsed twice in sterile bi-distilled water, for 5 min. Then, the seeds were sown individually into 0.25-l plastic pots (7 × 7 × 9 cm), filled with a professional substrate for vegetable seedlings composed of white peat, mixed peat fiber, wood chips, and mineral fertilizer according to the manufacturer's protocol; pH 5.6 (Profi-Substrat, Gramoflor GmbH & Co. KG, Vechta, Germany). Pots with seeds were maintained in a glasshouse (53°07'12.0"N 18°00'29.4"E) with a natural photoperiod.

On March 31, 2023, during the first leaf emergence phase, the uniformly developed plants were placed in a semi-sterile growth room with a controlled environment (20°C, 65% RH, 18-h photoperiod). Pots with plants were evenly distributed on shelves, with 50 plants per light treatment. Five different light treatments were tested (I–V) (Fig. 1). The Photosynthetic Photon Flux Density (PPFD) value was set at 50 µmol · m^{-2} · s^{-1} for all light treatments by adjusting the distance between the light source and the shelf surface using an FR-10 photometer (Optel, Opole, Poland) at the central point of an empty shelf. A spectroradiometer (Spectro Light, Łódź, Poland) was used to measure the light spectrum parameters (presented in Table 1 and Fig. 2).

The plants were grown for 21 days. The seedlings were watered daily but no fertilization or plant protection were applied. Next, a comparative analysis of the plants was carried out.

Analysis of plant morphology and biochemical activity

Whole plants were taken out of the pots, cleared of the substrate, and subjected to morphological measurements. Data, such as the shoot length (cm), shoot fresh weight (mg), shoot dry weight (mg), number of leaves, length of the longest root (cm), and root system fresh weight (mg), were collected. Subsequently, leaves
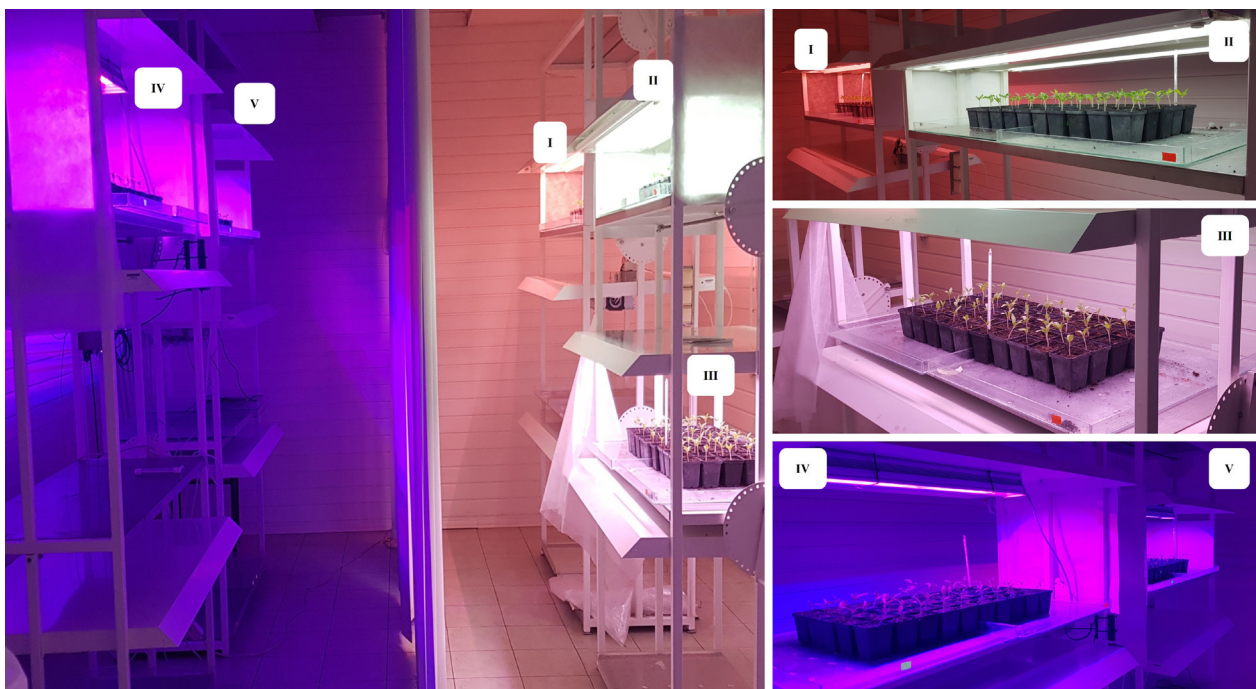

Fig. 1. Growth room with different light treatments (I–V) used in the experiment; general view (on the left), individual shelves (on the right). Treatments: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20)

Table 1. Characteristic of light treatments (I–V) used in the experiment

Light treatment	Light spectrum composition						Light source	Producer
	ultraviolet (UV) [%] 380–399 nm	blue (B) [%] 400–499 nm	green (G) [%] 500–599 nm	red (R) [%] 600–700 nm	far-red (FR) [%] 701–780 nm	R/B ratio		
I	0	11	20	61	8	5.55	AP673L LED tube T8	Valoya, Helsinki, Finland
II	1	29	46	21	3	0.72	TL-D 36W/54-765 fluorescent tube T8	Philips Amsterdam, Netherlands
III	0	32	25	38	5	1.19	FLUORA L 36W/77 fluorescent tube T8	OSRAM, Munich, Germany
IV	0	65	2	33	1	0.51	GROWLUX SOLUTIONS LED panel with PX241 LED Driver	PXM, Podłęże, Poland
V	0	81	2	16	1	0.20		
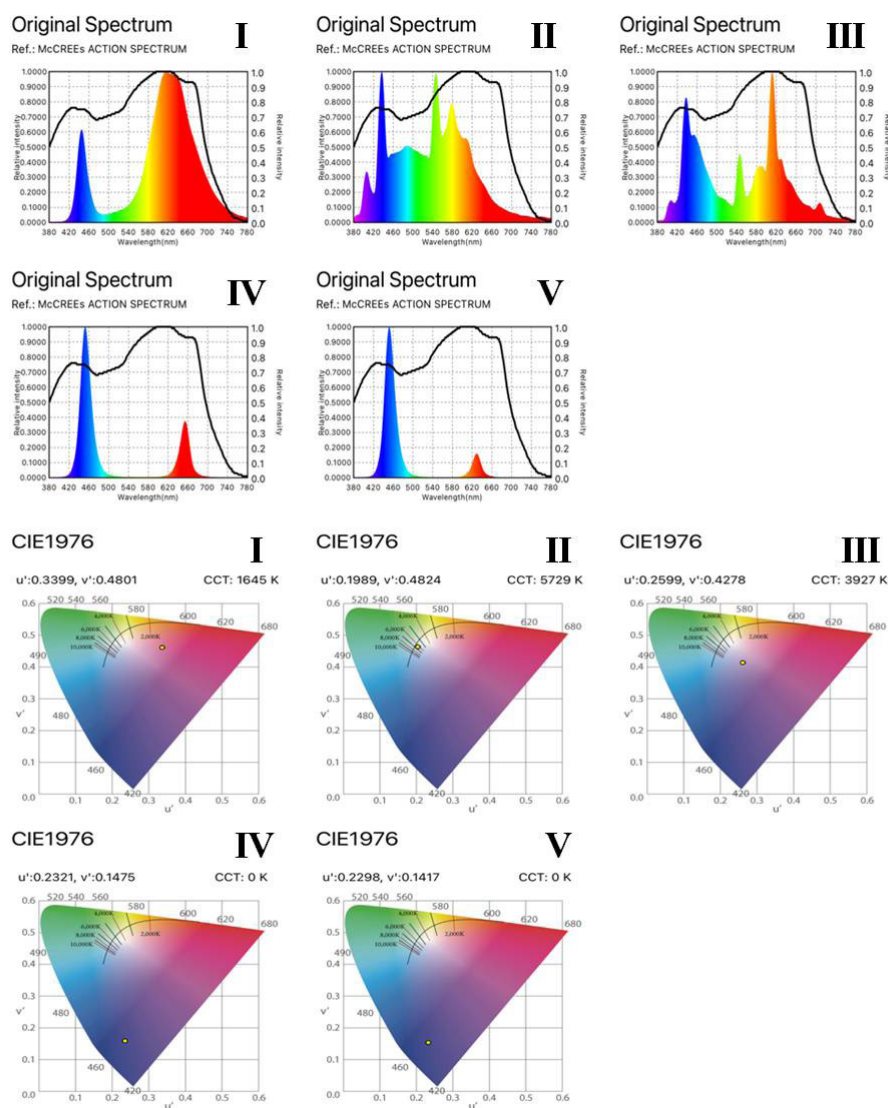
Fig. 2. Spectral characteristics of the light treatments (I–V) used in the experiment: action spectrum relative intensity (McCree 1971) (at the top) and calculated color temperature (CCT) (CIE 1976) (at the bottom). Treatments: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20)

and root systems were scanned (Epson STD4800 scanner, Suwa, Japan) and subjected to further biometric measurements, including the leaf area (cm^2), leaf perimeter (cm), maximal leaf vertical length (L) (cm), maximal leaf horizontal width (W) (cm), and leaf W/L ratio using the imaging software WinFOLIA™ (Reagen Instruments, Quebec, Canada), as well as the total length of root system (cm), root system area (cm^2), root diameter (mm), root system volume (cm^3), number of root tips, number of root forks, and number of root crossings using the imaging software WinRHIZO™ (Reagen Instruments, Quebec, Canada).

The whole leaves were used as fresh tissue samples for the biochemical assay. Chlorophyll *a* and *b*, and carotenoids were extracted by employing Lichtenthaler's (1987) method, utilizing 100 mg samples and 100% acetone (supplied by Chemia Sp. z o.o., Bydgoszcz, Poland). For anthocyanins (cyanidin-3-glucoside), 200 mg samples were treated with methanol containing 1% HCl (*v/v*) (Chemia Sp. z o.o., Bydgoszcz, Poland) based on the procedure of Harborne (1967). The same extract was utilized to determine the total phenolic content using the Folin-Ciocalteu protocol (Waterhouse 2001), employing gallic acid (Sigma-Aldrich, St. Louis, MO, USA) as the calibration standard.

To assess enzymatic activity, 100 mg samples were initially homogenized in a phosphate buffer (100 mM; pH 7.4) containing 1 mM EDTA, 1 mM dithiothreitol (DTT), and 2% (*w/v*) polyvinylpyrrolidone (PVP) (Chemat, Gdańsk, Poland), following the method outlined by Homaee and Ehsanpour (2016). After centrifugation (13,000× g for 20 min at 4°C) (Centrifuge MPW-260R, MPW MED INSTRUMENTS, Warsaw, Poland), the supernatants were utilized for determining total protein content (Bradford 1976) and the activities of specific antioxidant enzymes. Superoxide dismutase (SOD; EC 1.15.1.1) activity was assessed following the procedure of Giannopolitis and Ries (1977), while guaiacol peroxidase (GPOX; EC 1.11.1.7) activity was measured using the protocol modified by Nowogórska and Patykowski (2015) based on the Maehly and Chance (1954) method.

The SmartSpec Plus™ spectrophotometer (Bio-Rad, Hercules, CA, USA) was utilized for spectrophotometric assessments at specific wavelengths (λ_{max}): 530 nm for anthocyanins (cyanidin-3-glucoside), 645 and 662 nm for chlorophyll *a* and *b*, 470 nm for carotenoids, 765 nm for phenolics (gallic acid), 595 nm for proteins, 560 nm for SOD, and 470 nm for GPOX. Metabolite (chlorophyll *a* and *b*, carotenoids, anthocyanins, total phenolics) contents were computed per gram of a fresh weight (FW) sample (mg · g^{-1} FW), and SOD/GPOX enzymatic activity U (µmol · min^{-1}) was calculated per milligram of protein.

Analysis of plant resistance against fungal phytopathogens – detached leaf assay

The *Botrytis cinerea* and *Alternaria solani* isolates utilized in this study originated from the pathogenic fungi collection maintained at the Department of Biology and Plant Protection, Bydgoszcz University of Science and Technology, Poland. The *A. alternata* 1411 isolate originated from the Gene Bank of the Institute of Plant Protection – National Research Institute in Poznań. The pathogens demonstrated high pathogenicity to the tomato plants in a preliminary study (data not shown). Material for inoculation was prepared as follows: each pathogen was transferred from stored slants into Petri dishes filled with a potato dextrose agar (PDA) medium (BD Difco™, New Jersey, USA), acidified with 50% citric acid (4 ml per l) 1 week before the experiment. Dishes were incubated in darkness at 20−22°C. Following incubation, the spores produced by the mycelium were dispersed in distilled water. The concentration of colony-forming units (CFU) was microscopically assessed using a Thoma hemocytometer and adjusted to 1.5×10^{-6} CFU · ml^{-1}.

Assays were performed on tomato leaves detached from plants cultivated previously in the tested light treatments (I–V) for 3 weeks. Detached tomato leaves were washed with sterile water and placed on Whatman filter paper in Petri dishes soaked with 6 ml of sterile water to avoid dehydration. The leaves were inoculated with 10 µl drops of the pathogen's CFU suspensions. Dishes were sealed with Parafilm°M (Amcor, Zurich, Switzerland) and incubated under tested light treatments I–V. The percentage of the diseased area of the leaves infected with pathogens was visibly assessed after 7 days.

Statistical analysis

The experiment was set up in a completely randomized design. Each experimental object consisted of 50 plants forming individual repetitions (20 plants were designated to biometrical analysis, 10 plants to biochemical analysis, and 20 plants to analysis with fungal phytopathogens). To assess the impact of light treatments on observed traits, one-way analysis of variance (ANOVA) was performed. Mean values and standard deviations (SD) for traits were analyzed, and homogeneous groups were identified using Fisher's least significant differences (LSDs) at the 0.05 significance level. The analysis was performed using the Statistica 13.3 software package from StatSoft Polska, Cracow, Poland.

Results

Results of the biometrical analysis of the aerial parts of tomato plants showed that the best parameters in terms of shoot length, shoot fresh and dry weights, as well as the number of leaves were obtained in treatment I (AP673L LED tube T8), i.e. the one with the highest R/B ratio. High values of fresh weight were also found if treatment III was used (FLUORA L 36W/77 fluorescent tube T8). On the other hand, the lowest values of these parameters were found in treatments IV and V, i.e. those with a high blue light content. Likewise, plants grown under treatments IV and V had the least developed leaves with small leaf area, perimeter, vertical length, horizontal width and W/L ratio. The highest values of these parameters were reported in treatments I, II and III (leaf area and perimeter), treatments I and II (horizontal width and W/L ratio), as well as treatment III (vertical length) (Figs 3 and 4).

As for the root system, the highest fresh weight, area, length of the longest root, and total length of the root system, as well as the number of root tips and forks were found in treatments I and III. There were no differences between plants grown under treatments I–III in terms of root system volume and number of crossings. Root diameter was the least divergent as there were no differences between treatments I, II, IV and V. The least developed root systems were found in treatments IV and V, except for the root diameter, which was the lowest in plants grown under treatment III (Fig. 5).

The highest contents of chlorophyll *a*, chlorophyll *b*, chlorophylls (*a* + *b*), carotenoids, and anthocyanins were found in plants grown under treatment II. A distinctive content of chlorophyll *b* was also found in treatment III, while treatments I and III stimulated the biosynthesis of phenolic compounds. Generally,

tomato plants grown under lights with a high blue content (treatments IV and V) had the lowest concentration of pigments. There was no effect of light treatment on the activity of guaiacol peroxidase. On the other hand, the highest activity of SOD was detected in plants grown under light treatments I and II, while the lowest was with treatments IV and V, although it was not significantly different from treatment III (Table 2).

The tested light spectrum compositions affected pathogen development. Significant differences in leaf infection by the tested pathogens were observed in the light treatments. The severity of disease symptoms also varied depending on the pathogen species (Table 3).

The highest level of disease symptoms was recorded in *A. solani*. The most infected by this pathogen were leaves in treatments V and IV, in which the percentage of the surface with disease symptoms was 59.13% and 51.38%, respectively. Significantly lower infection was observed in treatments III and II, 15.13% and 13.48%, respectively. These treatments formed a statistically homogeneous group. The least susceptible to infection by this pathogen were leaves in treatment I, where the percentage of infection was 6.85%. The leaves of plants in treatments I and II were infected at a statistically similar level.

Alternaria alternata infected tomato leaves at a lower level than *A. solani*, not exceeding 18.13% in treatment IV. The leaves of plants in treatment V were infected at a slightly lower level of 15.88%. The occurrence of disease symptoms in these two treatments was at a statistically similar level and was significantly higher than in the other three light treatments. Leaves in treatment I were the least infected by *A. alternata*, at the level of 7.78%, creating a statistically homogeneous group with a combination of treatments II and III. The severity of disease symptoms in these treatments was 11.78% and 10.25%, respectively.

Fig. 3. *Solanum lycopersicum* L. 'Bawole Serce' seedlings after 3 weeks of cultivation in the growth room, depending on the light treatments (I–V) used in the experiment; bar = 5 cm. Treatments: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20)

Fig. 4. Parameters of the aerial parts of *Solanum lycopersicum* L. 'Bawole Serce' seedlings, depending on the light treatments (I–V) used in the experiment (means ± SD for each parameter followed by the same letter do not differ significantly at LSD$_{0.05}$). Treatments: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20)
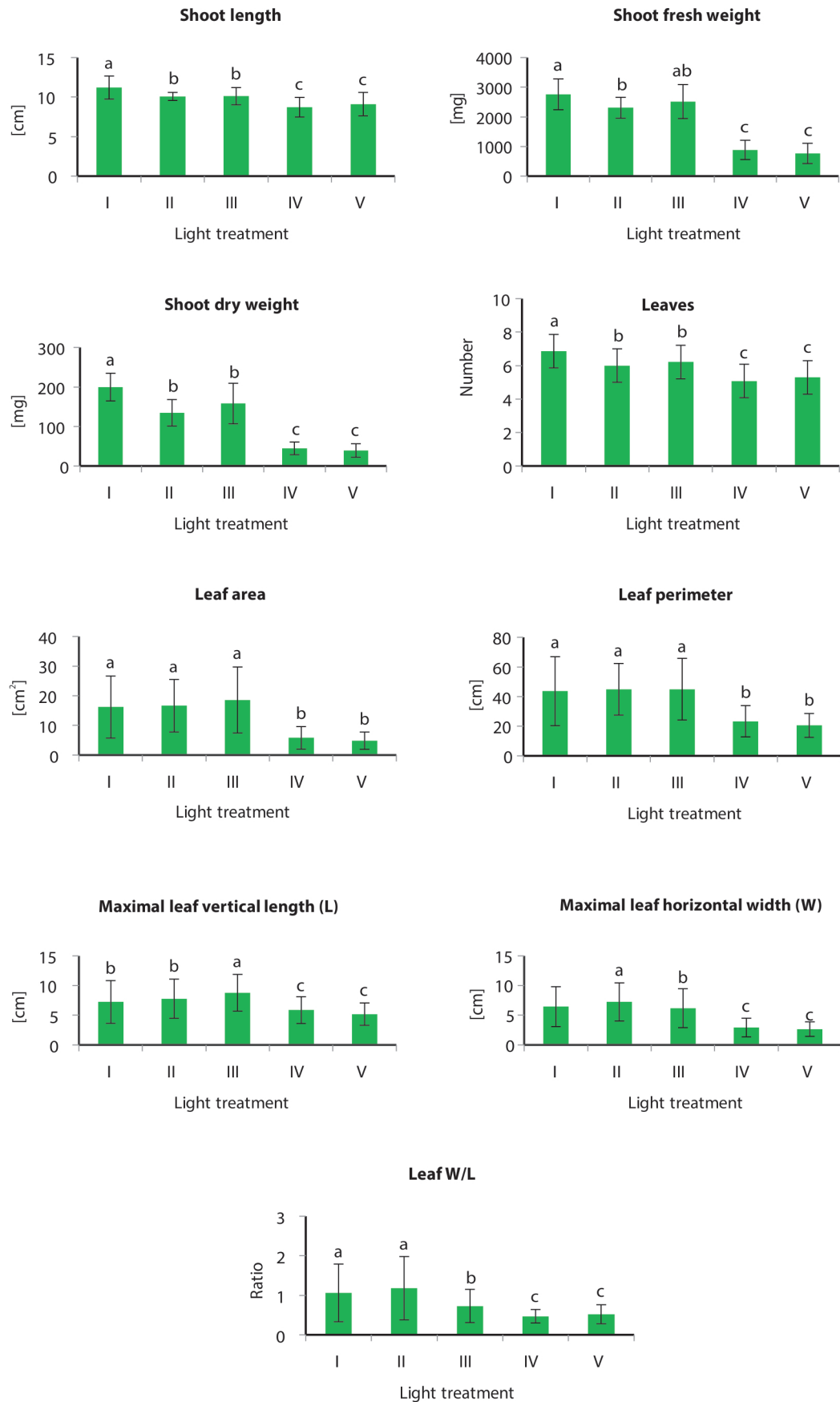
Root system fresh weight

Length of the longest root

Total length of root system

Root system area

Root diameter

Root system volume

Root tips

Root forks

Root crossings

Fig. 5. Parameters of the root system of *Solanum lycopersicum* L. 'Bawole Serce' seedlings, depending on the light treatments (I–V) used in the experiment (means ± SD for each parameter followed by the same letter do not differ significantly at LSD$_{0.05}$). Treatments: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20)
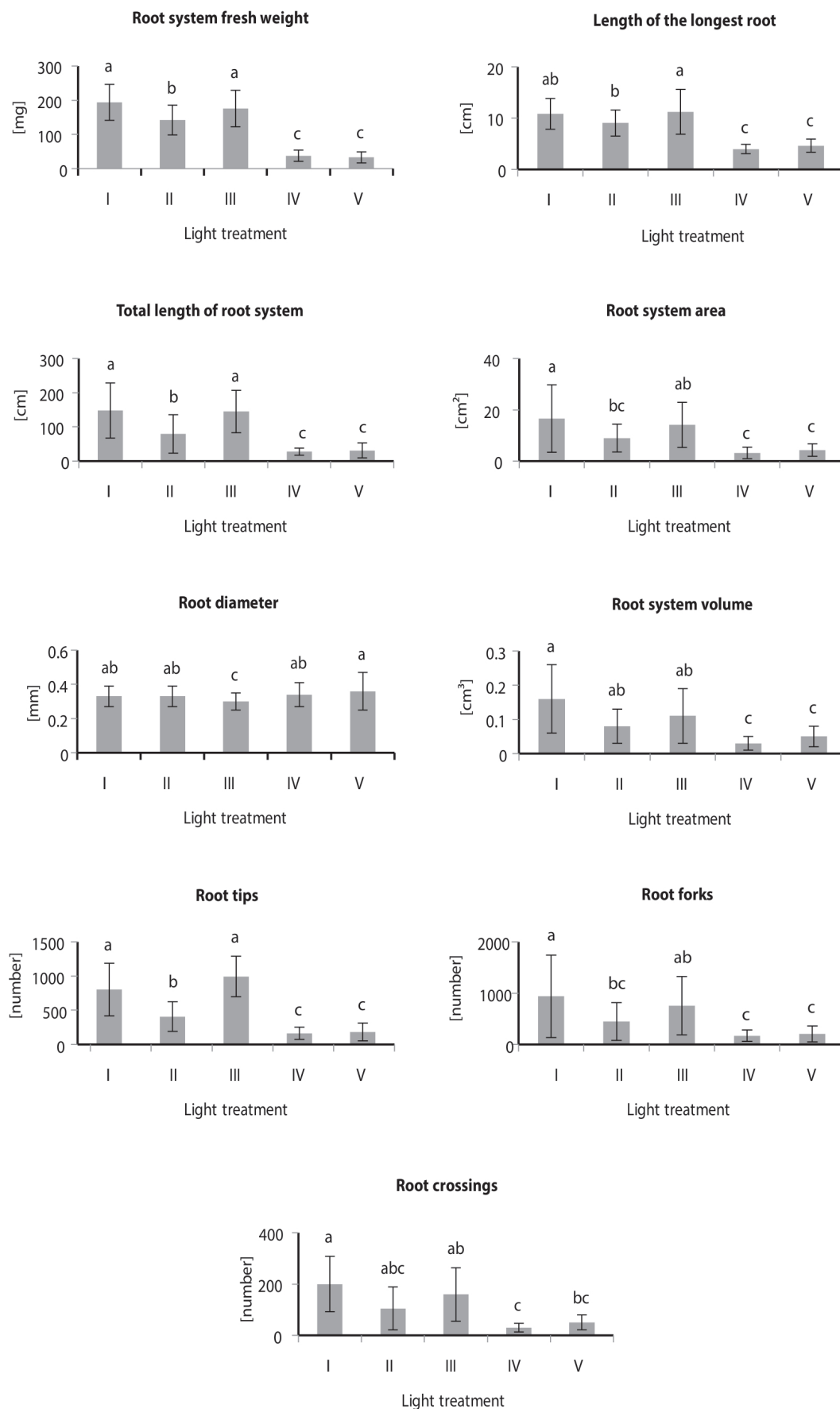
Table 2. Content of primary (chlorophyll *a*, chlorophyll *b*) and secondary (carotenoids, anthocyanins, phenolic compounds) metabolites, the activity of superoxide dismutase (SOD) and guaiacol peroxidase (GPOX) in *Solanum lycopersicum* L. 'Bawole Serce' seedlings, depending on the light treatments (I–V) used in the experiment. Treatments: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20)

Trait – biochemical assay	Light treatment				
	I	II	III	IV	V
Chlorophyll *a* content (mg · g^{-1} FW)	1.00 ± 0.13 b	1.25 ± 0.11 a	1.06 ± 0.05 b	0.61 ± 0.11 d	0.73 ± 0.08 c
Chlorophyll *b* content (mg · g^{-1} FW)	0.39 ± 0.05 b	0.45 ± 0.03 a	0.42 ± 0.04 ab	0.25 ± 0.05 c	0.28 ± 0.02 c
Chlorophylls (*a* + *b*) content (mg · g^{-1} FW)	1.39 ± 0.18 b	1.70 ± 0.14 a	1.48 ± 0.08 b	0.86 ± 0.16 c	1.01 ± 0.10 c
Carotenoids content (mg · g^{-1} FW)	0.22 ± 0.03 b	0.28 ± 0.02 a	0.24 ± 0.01 b	0.13 ± 0.03 c	0.16 ± 0.02 c
Anthocyanins content (mg · g^{-1} FW)	0.29 ± 0.06 b	0.35 ± 0.05 a	0.27 ± 0.02 b	0.18 ± 0.01 c	0.17 ± 0.03 c
Total phenolic content (mg · g^{-1} FW)	3.66 ± 0.26 abc	3.90 ± 0.40 a	3.86 ± 0.34 ab	3.40 ± 0.12 c	3.56 ± 0.15 bc
GPOX activity (U)	3.40 ± 0.61 a	3.36 ± 1.48 a	2.49 ± 0.82 a	3.41 ± 1.00 a	3.56 ± 1.89 a
SOD activity (U)	38.29 ± 6.95 ab	43.93 ± 8.18 a	34.06 ± 5.41 bc	30.32 ± 6.73 c	27.96 ± 4.29 c

Means ± SD in rows followed by the same letter do not differ significantly at LSD$_{0.05}$
FW – fresh weight

Table 3. Percentage of leaves diseased area in *Solanum lycopersicum* L. 'Bawole Serce' seedlings, depending on the light treatments (I–V) used in the experiment. Treatments: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20)

Phytopathogen	Light treatment				
	I	II	III	IV	V
Alternaria alternata	7.78 ± 4.74 b	11.78 ± 8 .00 b	10.25 ± 9.36 b	18.13 ± 12.84 a	15.88 ± 8.54 a
Alternaria solani	6.85 ± 6.09 c	13.48 ± 10.70 bc	15.13 ± 11.74 b	51.38 ± 22.42 a	59.13 ± 30.92 a
Botrytis cinerea	6.08 ± 7.22 c	13.75 ± 10.45 a	8.83 ± 10.91 abc	11.48 ± 12.59 ab	8.20 ± 13.67 bc

Means ± SD in rows followed by the same letter do not differ significantly at LSD$_{0.05}$

The lowest level of disease symptoms was observed in the experiment with *B. cinerea*. The average level of infection in treatments with this pathogen was 9.67% (*A. solani* – 29.19%, *A. alternata* – 12.76%). The highest level of leaf infection by *B. cinerea* occurred in treatments II, III and IV and amounted to: 13.75%, 8.83%, and 11.48%, respectively. These treatments created a statistically homogeneous group. The occurrence of disease symptoms was slightly lower in treatments I and V, 6.08% and 8.20%, respectively.

Discussion

In our research, tomato plants cultivated under light treatments with higher R/B ratio (I–III) presented generally higher shoot and root biometric parameters and had a higher content of metabolites than light treatments IV and V with a lower R/B ratio. Similarly, the fresh and dry weights of plants and leaf length in *Spinacia oleracea* L. were positively influenced by the irradiation with red light (629 nm) in comparison to white, blue (468 nm), and green (524 nm) light

(Battistoni *et al.* 2021). LED AP673L (treatment I in this study) was previously tested in another experiment and also significantly stimulated the vegetative growth of tomato and cucumber (*Cucumis sativus* L.) seedlings during indoor production (Tymoszuk *et al.* 2023). Taking into consideration the composition of the light spectra tested in this study, it can be presumed that light sources emitting wide spectrum light, consisting not only of blue, and red, but also green light, stimulate to a greater extent the plant vegetative growth and development in comparison to light sources with a low R/B ratio and a low share of green light in the emitted spectrum. Although green light is often regarded as the least efficient wavelength in the visible spectrum for photosynthesis, it has the ability to penetrate the tissues deeper than red or blue light and, consequently, boost the efficiency of photosynthesis. Studies have also confirmed that green light affects plant architecture (Liu and van Iersel 2021).

Considering the importance of tomato in human diets worldwide, studies on modern lighting systems in indoor cultivation are needed. Light affects plant growth and development, from seed germination to flowering,

by triggering various cellular responses resulting in physiological and metabolomic alternations of plants (He *et al.* 2022). Red light is mainly perceived by phytochromes, whereas blue light by cryptochromes and phototropins. Red and blue light are essential for photosynthesis. Red light most often stimulates plant growth by the induction of stem elongation, which was also confirmed in our study. On the other hand, blue light modulates phototropism, stomatal opening, chloroplast relocation, inhibition of hypocotyls elongation and leaf expansion, as well as regulating responses against biotic environmental stresses (Kim *et al.* 2013). Light can influence the production of secondary metabolites in tomato plants. For instance, specific blue light wavelengths, have been shown to enhance the accumulation of antioxidants, such as lycopene, carotenoids, phenolic compounds, flavonoids, and vitamin C, as well as overall antioxidant activity in tomato fruits (He *et al.* 2022). Nevertheless, such dependency was not confirmed in our study. Among the tested light spectrum compositions, treatment II was characterized by the highest share of green light (45%) in its spectrum, and plants cultivated under this light source had the highest concentration of evaluated primary (chlorophylls) and secondary (carotenoids, anthocyanins, phenolic compounds) metabolites. Interestingly, as reported by Zhang *et al.* (2020) supplementary red light also increased carotenoid content in tomato fruits. This could be linked with the elevated expressions of genes encoding ripening-related regulators and the biosynthesis of ethylene.

Our study revealed that plants from treatments I–III (with the highest R/B ratios) reached the highest biometric and biochemical parameters, including SOD activity and phenolic compounds content, and were simultaneously highly resistant to *A. alternata* and *A. solani* infection. In this case, proper growth processes and resistance to diseases were related traits. The lower susceptibility of tomato to both pathogens in these treatments could be a result of the higher production of SOD. This enzyme is considered the primary defense protein against oxidative burst – the result of biotic stress caused by pathogens (Das and Roychoudhury 2014). Therefore, it is recognized as the main component of the plant cell defense system against oxidative stress (Żuchowski 1999). Also, phenolic compounds are involved in plant defense mechanisms against infection by pathogens, e.g. *A. alternata* and *A. solani* (Dixon and Paiva 1995). These compounds are part of the plant's secondary metabolites and contribute to the reinforcement of cell walls, making it difficult for pathogens to penetrate. They can also directly inhibit the growth of pathogens by disrupting their cellular structures and metabolic processes. Moreover, phenolic compounds have antioxidant properties, which can counteract the oxidative stress imposed

by pathogens. Therefore, phenolic compounds are considered part of the broader spectrum of induced resistance mechanisms in plants against pathogens (Walters and Fountaine 2009).

In comparison to *Alternaria* spp. pathogens, the highest level of *B. cinerea* infection occurred in treatment II and was the lowest in treatment I (with the highest share of red light, 61%). In contrast to our results, monochromatic blue LED light (460 nm), compared to red (635 nm), green (520 nm) or white (420–680 nm) light, suppressed the development by *B. cinerea* the most, which was simultaneously accompanied by the intensified accumulation of phenolic compounds and increased activity of SOD and APX (ascorbate peroxidase) in tomato leaves and stems (Kim *et al.* 2013). On the other hand, red light (650–660 nm) and purple light (400–410 nm) inhibited *B. cinerea* infection in tomato. Interestingly, the disease suppression mechanisms of these two LED lights were different. While the red light inhibited gray mold predominantly by regulating the tomato defense mechanism (increased activity of superoxide dismutase, catalase and peroxidase), purple light caused the photo-inhibition of *B. cinerea* mycelium development (Hui *et al.* 2017). Contrary to our research, no biometric analysis of plants developed under the tested light spectra was provided in the above-mentioned studies, and simultaneous evaluation of plant architecture and resistance to pathogens was not presented.

Growers can optimize lighting conditions to enhance disease resistance and increase tomato plant growth and accumulation of beneficial secondary metabolites. Based on the obtained results, recommending treatment I for the production of tomato seedlings seems to be the most reasonable, due to the desired effects of the light spectral composition on plant growth, development and resistance to pathogens. Moreover, in treatment I, light was generated by a LED source, while in treatments II and III by fluorescent tubes. From a practical and economic perspective, LEDs have greater potential for horticultural production than fluorescent light sources, due to their longevity, better energy efficiency, flexibility of use, and lower heat generation (Miler *et al.* 2019).

Conclusions

Based on the obtained results of the effect of different light spectrum compositions: I (LED tube; R/B 5.55), II (fluorescent tube; R/B 0.72), III (fluorescent tube; R/B 1.19), IV (LED panel; R/B 0.51), V (LED panel; R/B 0.20), used in indoor cultivation on the growth, metabolite profile, and resistance of *Solanum lycoper-*

sicum 'Bawole Serce' seedlings against fungal phyto pathogens, it can be stated that:

1. The highest biometric parameters of aerial parts of plants were found in treatments I–III with higher R/B, as opposed to treatments IV and V with a high blue light content.

2. The best developed root systems were reported in treatments I and II, in contrast to treatments IV and V.

3. Generally, treatments I–III stimulated to a greater extent the accumulation of chlorophylls, carotenoids, anthocyanins and phenolic compounds, as well as the activity of superoxide dismutase when compared to treatments IV and V.

4. The level of *A. alternata* and *A. solani* disease symptoms was significantly higher for treatments IV and V than for I–III, whereas the highest/lowest level of *B. cinerea* infection was found in treatments II/I, respectively.

Light spectrum composition is of practical importance for tomato seedling indoor production. The precise control over light offers opportunities to promote plant productivity and resistance against phytopathogens. The knowledge gained from our study can be applied to improve production and disease management of tomato seedlings. In the future, it is worth continuing the research and evaluating the quality, yield and disease resistance of tomato plants developed from seedlings produced under the tested light treatments at further stages of cultivation.

References

Abdeldym E.A., El-Mogy M.M., Abdellateaf H.R.L., Atia M.A.M. 2020. Genetic characterization, agro-morphological and physiological evaluation of grafted tomato under salinity stress conditions. Agronomy 10 (12): 1948. DOI: https://doi.org/10.3390/agronomy10121948

Adhikari P., Oh Y., Panthee D.R. 2017. Current status of early blight resistance in tomato: an update. International Journal of Molecular Sciences 18 (10): 2019. DOI: https://doi.org/10.3390/ijms18102019

Amirahmadi E., Ghorbani M., Moudrý J., Konvalina P., Kopecký M. 2023. Impacts of environmental factors and nutrients management on tomato grown under controlled and open field conditions. Agronomy 13 (3): 916. DOI: https://doi.org/10.3390/agronomy13030916

Battistoni B., Amorós A., Tapia M.L., Escalona V. 2021. Effect of LED lights on the antioxidant properties of baby spinach leaves (*Spinacia oleracea* L.). Revista de la Facultad de Ciencias Agrarias – UNCuyo 53 (1): 98–108.

Bradford M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Analytical Biochemistry 72: 248–254. DOI: https://doi.org/10.1016/0003-2697(76)90527-3

CIE. 1976. https://cie.co.at/eilvterm/17-23-073

Courbier S., Snoek B.L., Kajala K., Li L., van Wees S.C.M., Pierik R. 2021. Mechanisms of far-red light-mediated dampening of defense against *Botrytis cinerea* in tomato

leaves. Plant Physiology 187 (3): 1250–1266. DOI: https://doi.org/10.1093/plphys/kiab354

Cuevas-Cianca S.I., Romero-Castillo C., Gálvez-Romero J.L., Juárez Z.N., Hernández L.R. 2023. Antioxidant and anti-inflammatory compounds from edible plants with anti-cancer activity and their potential use as drugs. Molecules 28 (3): 1488. DOI: https://doi.org/10.3390/molecules28031488

Das K., Roychoudhury A. 2014. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environ-mental stress in plants. Frontiers in Environmental Science 2: 53. DOI: https://doi.org/10.3389/fenvs.2014.00053

De Lucca A.J., Carter-Wientjes C., Williams K.A., Bhatnagar D. 2012. Blue light (470 nm) effectively inhibits bacterial and fungal growth. Letters in Applied Microbiology 55 (6): 460–466. DOI: https://doi.org/10.1111/lam.12002

DePhillipo N.N., Aman Z.S., Kennedy M.I., Begley J.P., Moatshe G., LaPrade R.F. 2018. Efficacy of vitamin C supplementation on collagen synthesis and oxidative stress after musculoskeletal injuries: A systematic review. Orthopedic Journal of Sports Medicine 6 (10): 2325967118804544. DOI: https://doi.org/10.1177/2325967118804544

Dixon R.A., Paiva N.L. 1995. Stress-induced phenylpropanoid metabolism. Plant Cell 7 (7): 1085–1097.

Dsouza A., Newman L., Graham T., Fraser E.D.G. 2023. Exploring the landscape of controlled environment agriculture research: A systematic scoping review of trends and topics. Agricultural Systems 209: 103673. DOI: https://doi.org/10.1016/j.agsy.2023.103673

El-Mansy A.B., Abd El-Moneim D., Alshamrani S.M., Safhi F.A., Abdein M.A., Ibrahim A.A. 2021. Genetic diversity analysis of tomato (*Solanum lycopersicum* L.) with morphological, cytological, and molecular markers under heat stress. Horticulturae 7 (4): 65. DOI: https://doi.org/10.3390/horticulturae7040065

Escobar-Bravo R., Chen G., Kim H.K., Grosser K., van Dam N.M., Leiss K.A., Klinkhamer P.G.L. 2019. Ultraviolet radiation exposure time and intensity modulate tomato resistance to herbivory through activation of jasmonic acid signaling. Journal of Experimental Botany 70 (1): 315–327. DOI: https://doi.org/10.1093/jxb/ery347

Fylladitakis E. 2023. Controlled LED lighting for horticulture: a review. Open Journal of Applied Sciences 13: 175–188. DOI: https://doi.org/10.4236/ojapps.2023.132014

Giannopolitis C.N., Ries S.K. 1977. Superoxide dismutases I. Occurrence in higher plants. Plant Physiology 59: 309–314. DOI: https://doi.org/10.1104/pp.59.2.309

Harborne J.B. 1967. Comparative biochemistry of the flavonoids. Phytochemistry 6 (11): 1569–1573. DOI: https://doi.org/10.1016/S0031-9422(00)82952-0

He R., Wei J., Zhang J., Tan X., Li Y., Gao M., Liu H. 2022. Supplemental blue light frequencies improve ripening and nutritional qualities of tomato fruits. Frontiers in Plant Science 13: 888976. DOI: https://doi.org/10.3389/fpls.2022.888976

Homaee M.B., Ehsanpour A.A. 2016. Silver nanoparticles and silver ions: oxidative stress responses and toxicity in potato (*Solanum tuberosum* L.) grown *in vitro*. Horticulture, Environment, and Biotechnology 57 (6): 544–553. DOI: https://doi.org/10.1007/s13580-016-0083-z

Hui X., Yan-nan F., Tian-lai L., Rui W. 2017. Effects of different LED light wavelengths on the resistance of tomato against *Botrytis cinerea* and the corresponding physiological mechanisms. Journal of Integrative Agriculture 16 (1): 106–114. DOI: https://doi.org/10.1016/S2095-3119(16)61435-1

Kim K., Kook H.-S., Jang Y.-J., Lee W.-H., Kamala-Kannan S., Chae J.-Ch., Lee K.-J. 2013. The effect of blue-light-emitting diodes on antioxidant properties and resistance to *Botrytis cinerea* in tomato. Journal of Plant Pathology & Microbiology 4 (9): 1000203. DOI: https://doi.org/10.4172/2157-7471.1000203

Lichtenthaler H.K. 1987. Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. Methods in Enzy-

mology 148: 350–382. DOI: https://doi.org/10.1016/0076-6879(87)48036-1

Liu J., van Iersel M.W. 2021. Photosynthetic physiology of blue, green, and red light: Light intensity effects and underlying mechanisms. Frontiers in Plant Science 12: 619987. DOI: https://doi.org/10.3389/fpls.2021.619987

Liu S., Yu L., Liu L., Yang A., Huang X., Zhu A., Zhou H. 2023. Effects of ultraviolet-B radiation on the regulation of ascorbic acid accumulation and metabolism in lettuce. Horticulturae 9 (2): 200. DOI: https://doi.org/10.3390/horticulturae9020200

Maehly A.C., Chance B. 1954. The assay of catalases and peroxidises. p. 357–425. In: "Methods of Biochemical Analysis" (D. Glick, ed.). John Wiley & Sons, Inc. DOI: https://doi.org/10.1002/9780470110171.ch14

Mazidi M., Ferns G., Banach M. 2020. A high consumption of tomato and lycopene is associated with a lower risk of cancer mortality: Results from a multi-ethnic cohort. Public Health Nutrition 23 (9): 1569–1575. DOI: https://doi.org/10.1017/S1368980019003227

McCree K.J. 1971. The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agricultural Meteorology 9: 191–216. DOI: https://doi.org/10.1016/0002-1571(71)90022-7

Meiramkulova K., Tanybayeva Z., Kydyrbekova A., Turbekova A., Aytkhozhin S., Zhantasov S., Taukenov A. 2021. The efficiency of LED irradiation for cultivating high-quality tomato seedlings. Sustainability 13 (16): 9426. DOI: https://doi.org/10.3390/su13169426

Miler N., Kulus D., Woźny A., Rymarz D., Hajzer M., Wierzbowski K., Nelke R., Szeffs L. 2019. Application of wide-spectrum light-emitting diodes in micropropagation of popular ornamental plant species: A study on plant quality and cost reduction. In Vitro Cellular and Developmental Biology – Plant 55: 99–108. DOI: https://doi.org/10.1007/s11627-018-9939-5

Nguyen T.-P.-D., Jang D.-C., Tran T.-T.-H., Nguyen Q.-T., Kim I.-S., Hoang T.-L.-H., Vu N.-T. 2021. Influence of green light added with red and blue LEDs on the growth, leaf microstructure and quality of spinach (*Spinacia oleracea* L.). Agronomy 11 (9): 1724. DOI: https://doi.org/10.3390/agronomy11091724

Nowogórska A., Patykowski J. 2015. Selected reactive oxygen species and antioxidany enzymes in common bean after *Pseudomonas syringae* pv. *phaseolicola* and *Botrytis cinerea* infection. Acta Physiologiae Plantarum 37: 1725. DOI: https://doi:10.1007/s11738-014-1725-3

Proietti S., Moscatello S., Riccio F., Downey P., Battistelli A. 2021. Continuous lighting promotes plant growth, light

conversion efficiency, and nutritional quality of *Eruca vesicaria* (L.) Cav. in controlled environment with minor effects due to light quality. Frontiers in Plant Science 12: 730119. DOI: https://doi.org/10.3389/fpls.2021.730119

Raiola A., Rigano M.M., Calafiore R., Frusciante L., Barone A. 2014. Enhancing the health-promoting effects of tomato fruit for biofortified food. Mediators of Inflammation 2014: 139873. DOI: https://doi.org/10.1155/2014/139873

Rasiukevičiūtė N., Brazaitytė A., Vaštakaitė-Kairienė V., Kupčinskienė A., Duchovskis P., Samuolienė G., Valiuškaitė A. 2021. The effect of monochromatic LED light wavelengths and photoperiods on *Botrytis cinerea*. Journal of Fungi 7 (11): 970. DOI: https://doi.org/10.3390/jof7110970

Soltis N.E., Atwell S., Shi G., Fordyce R., Gwinner R., Gao D., Shafi A., Kliebenstein D.J. 2019. Interactions of tomato and *Botrytis cinerea* genetic diversity: parsing the contributions of host differentiation, domestication, and pathogen variation. The Plant Cell 31 (2): 502–519. DOI: https://doi.org/10.1105/tpc.18.00857

Sotelo-Cardona P., Lin M.-Y., Srinivasan R. 2021. Growing tomato under protected cultivation conditions: overall effects on productivity, nutritional yield, and pest incidences. Crops 1: 97–110. DOI: https://doi.org/10.3390/crops1020010

Tymoszuk A., Kulus D., Błażejewska A., Nadolna K., Kulpińska A., Pietrzykowski K. 2023. Application of wide-spectrum light emitting diodes in the indoor production of cucumber and tomato seedlings. Acta Agrobotanica 76: 726. DOI: https://doi.org/10.5586/aa.762

Walters D.R., Fountaine J.M. 2009. Practical applications of induced resistance to plant diseases: an appraisal of effectiveness under field conditions. Journal of Agricultural Science 147 (5): 523–535

Wang S., Jin N., Jin L., Xiao X., Hu L., Liu Z., Wu Y., Xie Y., Zhu W., Lyu J., Yu, J. 2022. Response of tomato fruit quality depends on period of LED supplementary light. Frontiers in Nutrition 9: 833723. DOI: https://doi: 10.3389/fnut.2022.833723

Waterhouse A.L. 2001. Determination of total phenolics. p. I1.1.1–I1.1.8. In: "Current Protocols in Food Analytical Chemistry" (R.E. Wrolstad, ed.). John Wiley & Sons, Inc. DOI: https://doi.org/10.1002/0471142913.fai0101s06

Zhang J., Zhang Y., Song S., Su W., Hao Y., Liu H. 2020. Supplementary red light results in the earlier ripening of tomato fruit depending on ethylene production. Environmental and Experimental Botany 175: 104044. DOI: https://doi.org/10.1016/j.envexpbot.2020.104044

Żuchowski J. 1999. Vegetable superoxide dismutases. Kosmos 48 (1): 87–93 (in Polish)