

Leaf gas exchange, oxidative stress, and physiological attributes of rapeseed (*Brassica napus* L.) grown under different light-emitting diodes

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Abstract

Through its impact on morphogenesis, light is the key environmental factor that alters plant structural development; however, the understanding how light controls plant growth and developmental processes is still poor and needs further research. For this purpose, a Petri dish and pot experiment was conducted to investigate the effects of different LEDs, *i.e.*, white light (WL), red light (RL), blue light (BL), and orange light (OL) on morphology, gas-exchange parameters, and antioxidant capacity of *Brassica napus*. Compared with WL, RL significantly promoted plant growth and biomass, contents of photosynthetic pigments, and gas-exchange parameters in comparison to BL and OL. However, RL also helped decline malondialdehyde and proline contents and superoxide anion and peroxide production rate. In contrast, BL and OL significantly reduced plant growth and biomass, gas-exchange attributes and increased the activities of superoxide dismutase and peroxidase in Petri dish as well as in pot experiment. These results suggest that red light could improve plant growth in *B. napus* plants through activating gas-exchange attributes, reduce reactive oxygen species accumulation, and promote antioxidant capacity.

Additional key words: antioxidative enzymes; light quality; photosynthesis.

Introduction

Light and temperature are essential environmental factors affecting the plant survival, distribution of dry mass, and crop yield (Rehman *et al.* 2017, Saleem *et al.* 2019b). Plants are exposed to a variety of environmental factors including low and high temperatures, light intensity, alkalinity, acidity, drought, and oxidative damage (Fahad and Bano 2012, Fahad *et al.* 2013, 2014a,b; 2015a,b; 2016a,b,c,d; 2017, 2018, 2019a,b; Saud *et al.* 2016, 2017a,b). Various factors, such as temperature, light, pH, aeration, and agitation affecting the production of metabolites have been studied extensively (Fukuda *et al.* 2008, Haliapas *et al.* 2008, Janda *et al.* 2014, Yu *et al.* 2017, Sytar *et al.* 2019). Specifically, changes in light quality

due to the spectral properties of tissue pigments strongly affect plant anatomical, physiological, morphological, and biochemical parameters of leaves (Zhao *et al.* 2012, 2018; Saud *et al.* 2014, Rehman *et al.* 2017). The sound effects of light are diverse and significant to the long-term survival of food specialty crop species (Urbonavičiūtė *et al.* 2007, Nanya *et al.* 2012, Zhao *et al.* 2013a). Quality of light or modulating wavelengths, which are detected by phytochromes in plants, can cause changes in morphology and development (Kami *et al.* 2010, Zhao *et al.* 2013b). The spectrum of visible light is formed by red, orange, yellow, green, blue, indigo, and violet. Far-red light is essential for stimulating flowering in long-day plants (Shimizu *et al.* 2011, Kobayashi *et al.* 2013). Blue light induces stomatal opening and deactivates guard cell solute uptake in a

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Abbreviations: BL – blue light; C_i – intercellular CO₂ concentration; E – transpiration rate; g_s – stomatal conductance; LED – light-emitting diodes; MDA – malondialdehyde; OL – orange light; P_N – net photosynthesis; POD – peroxidase; RL – red light; ROS – reactive oxygen species; SOD – superoxidase dismutase; WL – white light.

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wide range of plant species (Evans and Halliwell 2001, Trouwborst *et al.* 2010). Orange light reduces plant growth and CO₂ assimilation (Wang *et al.* 2001, Cope and Bugbee 2013). LEDs are solid-state semiconductors that produce a narrow spectrum and noncoherent light and are much more efficient than any glass-envelope lamp (Singh *et al.* 2015, Rehman *et al.* 2017). LEDs can have peak emission wavelengths from ~250 nm (UV) to ~1,000 nm (infrared) with more efficient performance and longevity well beyond any traditional lighting system (Bourget 2008, Morrow 2008).

Stress conditions can disturb the dynamic equilibrium of reactive oxygen species (ROS) production and elimination under normal growth in plants (Rizwan *et al.* 2016) which promotes ROS accumulation, membrane lipid peroxidation, and disrupt the structure and function of cell membrane system (Sgherri *et al.* 2007, Quartacci *et al.* 2015, Rehman *et al.* 2019a, Saleem *et al.* 2019a, Kamran *et al.* 2020a). ROS, such as superoxide radical, H₂O₂, singlet oxygen (¹O₂), and hydroxyl radicals (OH) in plants are removed by a variety of antioxidant enzymes, such as superoxidase dismutase (SOD, EC 1.15.1.1.) and peroxidase (POD, EC 1.11.1.x) (Lee *et al.* 2003, Wu *et al.* 2007, Mastropasqua *et al.* 2012, Rehman *et al.* 2019b, Rana *et al.* 2020, Saleem *et al.* 2020c). Rapeseed (*Brassica napus* L.) is sensitive to light quality. The factory production of rapeseed seedlings for vegetable use and for transplanting in the field requires an investigation of the responses of *B. napus* to light quality (Li *et al.* 2012, Thiyam-Holländer *et al.* 2014, Zhang *et al.* 2015, Chang *et al.* 2016, Wu and Ma 2018, Khan *et al.* 2019). *B. napus* is the second largest oil crop in the world, and China ranks the second place in the world in the production of *B. napus* (FAOSTAT 2013). A plant factory with LEDs may provide high precision and standardization of *B. napus* plants for transplanting and vegetable cultivation. However, *B. napus* is very sensitive to the light quality (Li *et al.* 2012, Chang *et al.* 2016), and its responses to light quality should be investigated before the LEDs are applied in the plant factory. The aim of the present study was to quantify and compare the influences of varying light quality on biomass, photosynthetic capacity, photosynthetic pigment content, gas-exchange attributes, as well as ROS production and antioxidant enzyme activities of *B. napus* plants. Findings from the study are needed for better understanding morphological and physiological responses of plants to differential light quality. Additionally, this research can aid in designing the appropriate light environment to promote the growth of *B. napus* plants and to provide a theoretical basis for standardized cultivation of oil seed plant.

Materials and methods

Petri dish experiment was conducted under glasshouse environment using different LEDs (100 W, Dongri Optics Technology Co., Ltd., Dongguan, Guangdong Province, China) with day and night temperature range (2–10°C) outside and humidity of 80–90% in Huazhong Agricultural University Wuhan, China (114.20°E, 30.28°N; 50 m a. s. l.) in October 2017. Ten seeds of ‘Huaza No. 5’ (released

from Bast and Fiber Research Center of Huazhong Agricultural University) were used for each Petri dish (90 mm in diameter). Seeds were surface-sterilized with 10% (v/v) commercial bleach for 15 min followed by a thorough washing in distilled water for the prevention of surface fungal/bacterial contamination. Each Petri dish was then placed under different LEDs. The wavelengths of different LEDs were WL (400 nm), RL (660 nm), BL (450 nm), and OL (610 nm) as shown in (Fig. 1) and measured by LI6400 (Li-Cor, Nebraska, USA). The Petri dish experiment was performed in completely randomized design (CRD) with three replicates for each treatment. All plants were harvested after 21 d after sowing (DAS) and different morphological traits and sampling were taken for physiological analysis. All chemicals used were of analytical grade, procured from Sinopharm Chemical Reagent Co., Ltd., China.

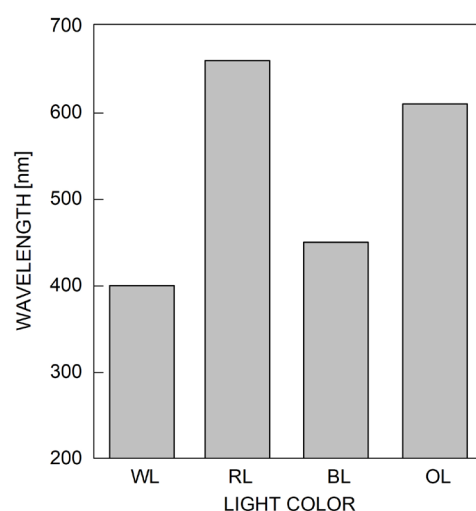


Fig. 1. Relative radiance of plastic filter used: WL (white light), RL (red light), BL (blue light) and OL (orange light).

Pot experiment: In late October 2017, a pot experiment started using pots (30-cm-tall × 20-cm-wide) having 10 kg of natural soil (obtained from different experimental stations of Huazhong Agricultural University, Wuhan, China). Physicochemical properties of natural soil used for pot experiment were of pH 5.6, EC of 1.98 dS cm⁻¹, 23 mg(organic matter) kg⁻¹, 58 mg(exchangeable K) kg⁻¹, 39 mg(exchangeable N) kg⁻¹, and 0.16 mg(exchangeable P) kg⁻¹. Pots were placed under natural light (sunlight) and after germination of seeds (21 DAS), pots were shifted under different LEDs. Ten seeds were sown in each pot, which were then thinned to three plants and three pots were placed under each LED with three replications. N, P, and K (complex) were given to each pot as recommended by Kamran *et al.* (2020a). Deionized water was added and soil-water suspension was maintained (w/v, 1:2.5); thinning and other necessary intercultural operations were carried out as necessary. Pots were placed in a glasshouse, where plants received natural light, with day/night temperature of 2–10°C and day/night humidity of 80/90%.

Sampling for different physiological attributes was done at 60 DAS and all plants were harvested on 5 March 2018.

Sampling and data collection: For Petri dish experiment, all seedlings were harvested at 21 DAS, while for pot experiment, all plants were harvested at 150 DAS. Fresh leaves from each treatment were harvested at a rapid growth stage during 09:00–10:30 h. The sampled leaves were washed with distilled water, immediately placed in liquid nitrogen, and stored in a freezer at low temperature (-80°C) for further analysis. Plants were randomly selected to measure their height, fresh and dry mass. Height was measured with the help of measurement scale. Stem diameter (mm) was measured by using digital Vernier caliper (*ST22302SG Tools*, Hangzhou, China) above 10 cm from the soil surface. The *B. napus* shoots and roots were washed with deionized water to remove the adhered soil and dried on filter paper. The fresh biomass of shoots and roots was calculated by using a digital balance with 0.001 g accuracy. Afterwards, plant tissues were oven dried (model 100-800, *Memmert GmbH*, Schwabach, Germany) at 67°C until they reached a constant mass to determine dry biomass.

Photosynthetic pigments and gas-exchange parameters: For the analysis of chlorophyll (Chl) contents, 0.1 g of fresh leaf sample was extracted with 8 mL of 95% acetone for 24 h at 4°C in darkness. The absorbance was measured by a spectrophotometer (*Shimadzu UV-2550*, Kyoto, Japan) at 646.6, 663.6, and 450 nm. Chl contents were calculated by the standard method of Arnon (1949) and expressed in mg g^{-1} (fresh mass, FM).

Gas-exchange parameters were measured using a portable photosynthesis system *Li-6400* (*Li-COR*, Lincoln, NE, USA): net photosynthesis (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i). These parameters were measured during 10:00–11:00 h when all plant parts were fully functional.

Malondialdehyde (MDA), proline, and antioxidant enzyme activities: The degree of lipid peroxidation was evaluated as malondialdehyde (MDA) contents. Frozen leaves of 0.1 g were ground at 4°C in a mortar with 25 mL of 50 mM phosphate buffer solution (pH 7.8) containing 1% polyvinylpyrrolidone (PVP). The homogenate was centrifuged at $10,000 \times g$ at 4°C for 15 min. The mixtures were heated at 100°C for 15–30 min and then quickly cooled in an ice bath. The absorbance of the supernatant was recorded by using spectrophotometer (*xMark™* microplate absorbance spectrophotometer, *BioRad*, USA) at the wavelengths of 532, 600, and 450 nm. Lipid peroxidation was calculated using the following formula: $6.45 (A_{532} - A_{600}) - 0.56 A_{450}$ and expressed in mg(MDA) g^{-1} (FM). The method was followed by Heath and Packer (1968).

Proline contents were measured by using (0.1 g) homogenate in 3% of aqueous sulphosalicylic acid and distilled water. The proline content was assessed by the technique described by Bates *et al.* (1973) and expressed in mg g^{-1} (FM).

In order to check enzyme activities, fresh leaves (0.5 g) were homogenized in liquid nitrogen and 5 mL of 50 mM sodium phosphate buffer (pH 7.0) including 0.5 mM EDTA and 0.15 mM NaCl. The homogenate was centrifuged at $12,000 \times g$ for 10 min at 4°C , and the supernatant was used for measurement of SOD and POD activities.

The SOD activity was assayed in 3 mL of reaction mixture containing 50 mM sodium phosphate buffer (pH 7), 56 mM nitroblue tetrazolium (NBT), 1.17 mM ribofavin, 10 mM methionine, and 100 μL of enzyme extract. Finally, reading was taken by using spectrophotometer (*xMark™* microplate absorbance spectrophotometer, *Bio-Rad*, USA). We followed the method by Chen and Pan (1996); SOD activity was expressed as U g^{-1} (FM).

POD activity in leaves was estimated using the method of Sakharov and Aridilla (1999) and was assayed using guaiacol as the substrate. The reaction mixture (3 mL) contained 0.05 mL of enzyme extract, 2.75 mL of 50 mM phosphate buffer (pH 7.0), 0.1 mL of 1% H_2O_2 , and 0.1 mL of 4% guaiacol solution. The increase in the absorbance at 470 nm due to guaiacol oxidation was recorded for 2 min. One unit of enzyme activity was defined as the amount of the enzyme causing a change in absorbance of 0.01 per min. The specific POD activity was expressed as U g^{-1} (FM).

Statistical analysis: All results were presented as arithmetic means with standard deviation except otherwise defined. One-way analysis of variance (*ANOVA*) was performed with LSD test at $p \leq 0.05$ to measure differences in variables between the different treatments followed by LSD test to compare with treatments means using *Statistix 8.1*. Graphical presentation was carried out using *SigmaPlot 10*. The *Pearson's* correlation coefficients between the measured variables of rapeseed were also calculated using *R Studio*.

Results

The results of present study revealed that different quality of lights induced different growth and biomass in *B. napus* seedlings and plants. In Petri dish experiment, different morphological traits, *i.e.*, seedling length, root length, shoot length, and seedling fresh mass were measured (Table 1). The results depicted that seedling length increased under RL by 29.2% when compared with WL (control treatment). The maximum seedling length was 8.4 cm when plants grew under RL, while the minimum seedling length was 3.38 cm when plants were grown under OL compared with WL. In the same way, maximum seedling fresh mass was observed in plants when grown under RL (3.1 g per seedling), while minimum fresh mass was observed in OL (2.0 g per seedling) compared with WL. These results suggested that RL improved seedling growth and biomass, while BL and OL reduced growth when compared with WL.

In pot experiment, different morphological traits, such as plant height, root length, crown length, plant diameter, root diameter, number of branches, number of leaves, plant fresh mass, leaf fresh mass, plant dry mass, stem dry mass,

Table 1. Effect of different colors of light on seedling height, root length, shoot length, and total fresh mass in Petri dish experiment on *Brassica napus*. Data are the average of three replications $\pm$ SD. Different letters within a column indicate significant difference between the treatments ($P < 0.05$ or $P < 0.01$). Relative radiance of plastic filter used: WL (white light), RL (red light), BL (blue light) and OL (orange light).

Light	Seedling height [cm]	Root length [cm]	Shoot length [cm]	Total fresh mass [g]
WL	6.50 $\pm$ 0.12 ^b	1.53 $\pm$ 0.03 ^b	4.97 $\pm$ 0.12 ^b	2.70 $\pm$ 0.06 ^b
RL	8.42 $\pm$ 0.12 ^a	1.80 $\pm$ 0.06 ^a	6.67 $\pm$ 0.09 ^a	3.10 $\pm$ 0.06 ^a
BL	4.52 $\pm$ 0.12 ^c	1.27 $\pm$ 0.03 ^c	3.30 $\pm$ 0.06 ^c	2.63 $\pm$ 0.03 ^b
OL	3.38 $\pm$ 0.15 ^d	0.93 $\pm$ 0.03 ^d	2.50 $\pm$ 0.06 ^d	2.00 $\pm$ 0.06 ^d

Table 2. Effect of different colors of light on plant height, root length, plant diameter, root diameter, crown length, number of branches, and number of leaves in pot experiment on *Brassica napus*. Data are the average of three replications $\pm$ SD. Different letters within a column indicate significant difference between the treatments ($P < 0.05$ or $P < 0.01$). Relative radiance of plastic filter used: WL (white light), RL (red light), BL (blue light) and OL (orange light).

Light	Plant height [cm]	Root length [cm]	Plant diameter [mm]	Root diameter [mm]	Crown length [cm]	Branches [per plant]	Leaves [per plant]
WL	106 $\pm$ 3 ^b	11.0 $\pm$ 1.0 ^b	10.0 $\pm$ 0.1 ^c	10.0 $\pm$ 0.3 ^b	31 $\pm$ 1 ^b	8.0 $\pm$ 0.3 ^b	60 $\pm$ 1 ^b
RL	120 $\pm$ 2 ^a	16.0 $\pm$ 0.4 ^a	10.0 $\pm$ 0.1 ^c	8.0 $\pm$ 0.4 ^c	41 $\pm$ 1 ^a	10.0 $\pm$ 0.3 ^a	74 $\pm$ 1 ^a
BL	93 $\pm$ 1 ^c	9.0 $\pm$ 0.2 ^c	13.0 $\pm$ 0.3 ^a	12.0 $\pm$ 0.5 ^{ab}	26 $\pm$ 1 ^b	7.0 $\pm$ 0.6 ^b	51 $\pm$ 1 ^c
OL	81 $\pm$ 1 ^d	6.0 $\pm$ 0.2 ^d	14.0 $\pm$ 0.6 ^a	14.0 $\pm$ 0.6 ^a	18 $\pm$ 1 ^c	4.0 $\pm$ 0.3 ^c	34 $\pm$ 1 ^d

Table 3. Effect of different colors of light on plant fresh mass (FM), leaves FM, plant dry mass (DM), leaves DM, and stem DM in pot experiment on *Brassica napus*. Data are the average of three replications $\pm$ SD. Different letters within a column indicate significant difference between the treatments ($P < 0.05$ or $P < 0.01$). Relative radiance of plastic filter used: WL (white light), RL (red light), BL (blue light) and OL (orange light).

Light	Plant FM [g]	Leaves FM [g]	Plant DM [g]	Leaves DM [g]	Stem DM [g]
WL	198 $\pm$ 1 ^b	90 $\pm$ 3 ^b	105 $\pm$ 2 ^b	9.0 $\pm$ 0.1 ^b	10.0 $\pm$ 0.2 ^b
RL	235 $\pm$ 10 ^a	112 $\pm$ 3 ^a	126 $\pm$ 2 ^a	11.0 $\pm$ 0.5 ^a	12.0 $\pm$ 0.2 ^a
BL	176 $\pm$ 1 ^b	79 $\pm$ 2 ^c	91 $\pm$ 4 ^b	8.0 $\pm$ 0.1 ^{bc}	6.0 $\pm$ 0.1 ^c
OL	115 $\pm$ 3 ^c	51 $\pm$ 2 ^d	65 $\pm$ 2 ^c	6.0 $\pm$ 0.1 ^c	3.0 $\pm$ 0.1 ^d

and leaf dry mass were measured (Tables 2, 3). Maximum plant height and crown length was observed in the plants when grown in RL and increased by 13.2 and 32.2%, respectively, when compared with WL. The maximum plant height was 120 cm and crown length was 41 cm in the plants grown under RL. Similarly, the highest amount of fresh and dry biomass was observed when grown under RL and the lowest when grown under OL and BL. The maximum plant fresh mass and dry mass increased by 18.6 and 20%, respectively, when plants were grown in RL compared with WL. However, maximum fresh mass was 235 g per plant and maximum dry mass was 126 g per plant in plants grown under RL compared with WL.

Different LEDs resulted in difference in the contents of total chlorophyll (Chl) and carotenoids (Fig. 2). The results from present study depicted that RL significantly increased total Chl and carotenoid contents, while BL and OL reduced these contents when compared with WL. For Petri dish experiment, the contents of total Chl and carotenoids increased by 17.5 and 20.4%, respectively, under RL, while the contents of total Chl and carotenoids were reduced by 9.2 and 15.9%, respectively, under OL

when compared with WL. The maximum contents of total Chl and carotenoids were observed in plants grown under RL which were 2.4 and 0.53 mg g⁻¹(FM), while minimum contents of total Chl and carotenoids were observed in plants grown under OL [1.8 and 0.35 mg g⁻¹(FM)] when compared with WL.

The similar pattern for total Chl and carotenoids was also observed in the pot experiment (Fig. 2). RL significantly increased total Chl and carotenoids, while BL and OL reduced these contents when compared with WL. The contents of total Chl and carotenoids increased by 11.9 and 9.1%, respectively, under RL, while the contents of total Chl and carotenoids were reduced by 27.9 and 53.2%, respectively, under OL when compared with WL. The maximum contents of total Chl and carotenoids were observed in plants grown under RL, which were 2.72 and 0.84 mg g⁻¹(FM), while minimum contents of total Chl and carotenoids were observed in plants grown under OL, i.e., 1.75 and 0.36 mg g⁻¹(FM) when compared with WL.

Different gas-exchange parameters for the pot experiment exhibited different response when plants were grown under different LEDs (Fig. 3). The maximum value for

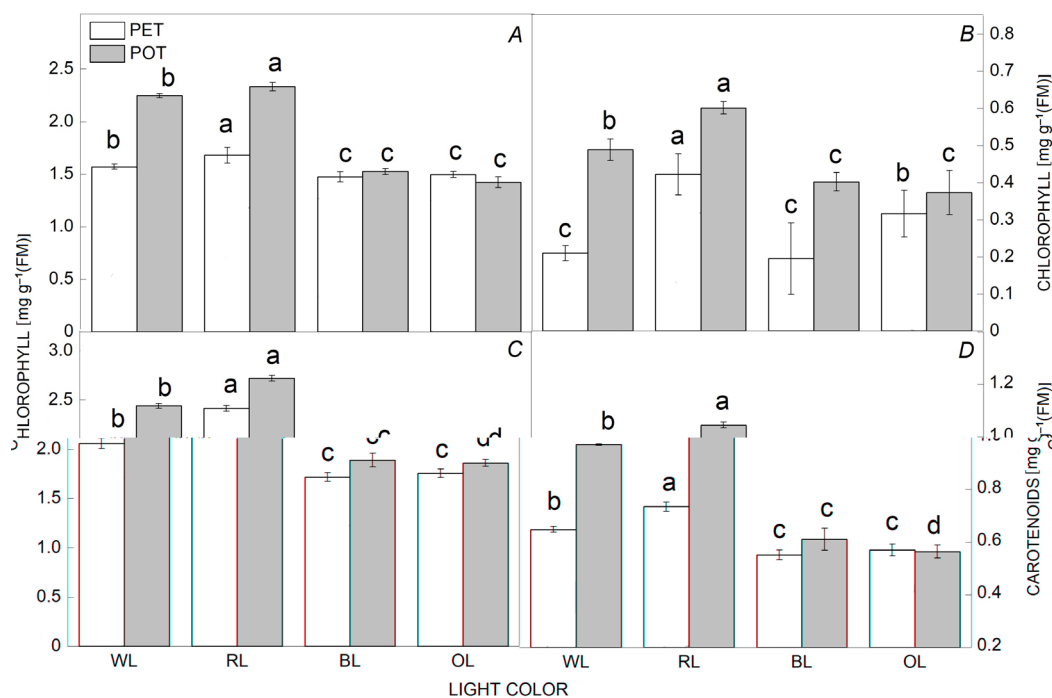


Fig. 2. Influence of different colors of light on chlorophyll *a* (A), chlorophyll *b* (B), total chlorophyll (C), and carotenoids (D) of *Brassica napus*. Relative radiance of plastic filter used: WL (white light), RL (red light), BL (blue light), and OL (orange light). Different letters indicate statistical differences ($P \leq 0.05$) or ($P \leq 0.01$) according to an LSD test. Data are the average of three replications $\pm$ SD. PET – Petri dish experiment; POT – pot experiment.

P_N , E , g_s , and C_i were observed in the plants when grown under RL compared with WL. Under RL, P_N increased by 28.8%, E increased by 14.6%, g_s increased by 15.1%, and C_i increased by 8.6% when compared with WL. However, the minimum value of P_N was $6.3 \mu\text{mol m}^{-2} \text{s}^{-1}$, E was $6.3 \text{ nmol m}^{-2} \text{s}^{-1}$, g_s was $0.14 \text{ mmol m}^{-2} \text{s}^{-1}$, and C_i was $204 \mu\text{mol mol}^{-1}$ in plants grown under OL compared with WL.

In the present study, the effect of different LEDs on lipid peroxidation, contents of proline, and antioxidant enzymes in *B. napus* were also investigated (Fig. 4). The results depicted that plants grown under BL and OL significantly increased MDA contents in the leaves which indicated that BL and OL induced oxidative damage in *B. napus*. In the Petri dish experiment, the contents of MDA increased by 22.6 and 12.2% when plants were grown in BL and OL, respectively, compared with WL. In the same way, maximum contents of proline were observed in plants grown under BL and OL, *i.e.*, 36 and $40 \mu\text{g g}^{-1}(\text{FM})$, respectively, compared with WL. It was also observed that enzymatic activities of SOD and POD increased in plants grown under BL and OL compared with WL (Fig. 4C,D). The maximum activity of SOD increased by 15.1 and 14.7%, respectively, while POD activity increased by 19.3 and 17.7%, respectively, when plants were grown under BL and OL compared with WL. The minimum activity of SOD and POD was observed in plants grown under RL, *i.e.*, 62 and $2,200 \text{ U g}^{-1}(\text{FM})$, respectively, compared with WL.

In the pot experiment, BL and OL also caused severe damage to the membrane of lipids compared with WL (Fig. 4A). Results from the present experiment depicted that the contents of MDA increased by 20.3 and 17% in plants grown under BL and OL, respectively, which showed that BL and OL caused oxidative damage in the leaves of *B. napus*. Proline content increased by 68.4 and 103.6% in plants grown under BL and OL compared to WL. The maximum contents of proline were observed in plants grown under BL and OL, 41 and $49.7 \mu\text{g g}^{-1}(\text{FM})$ compared with WL. The enzymatic activity was also investigated for the pot experiment and results depicted that SOD activity increased by 15.6 and 16%, respectively, while POD activity increased by 25.7 and 64.3%, respectively, in plants grown under BL and OL compared with WL.

The Pearson's correlation analysis was carried out to quantify the relationship between various studied parameters (Fig. 5). Plant height was positively correlated with other growth attributes, photosynthetic pigments, and gas-exchange parameters, while negatively correlated with total diameter and root diameter of the plant. Total diameter of plant was positively correlated with root diameter while negatively correlated with all other growth parameters, photosynthetic pigments, and gas-exchange parameters. This correlation reflected the close connection between growth parameters, photosynthetic pigments, and gas-exchange parameters in *B. napus*.

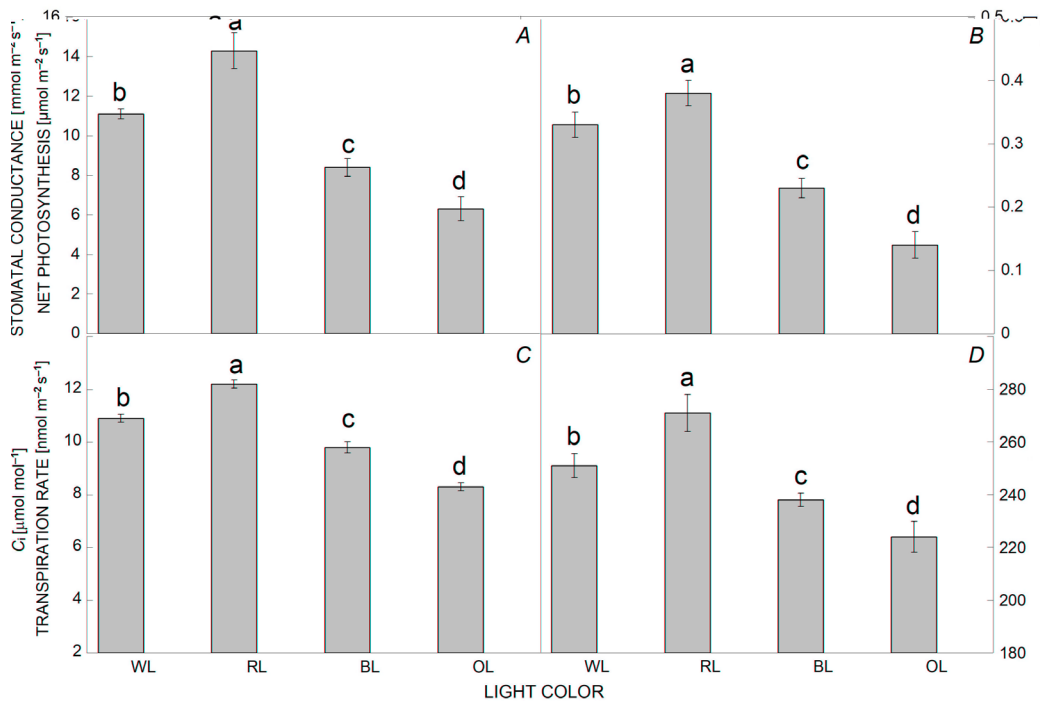


Fig. 3. Influence of different colors of light on net photosynthesis (A), stomatal conductance (B), transpiration rate (C), and intercellular CO_2 concentration (D) in *Brassica napus* of pot experiment. Relative radiance of plastic filter used: WL (white light), RL (red light), BL (blue light) and OL (orange light). Different letters indicate statistical differences ($P \leq 0.05$) or ($P \leq 0.01$) according to an LSD test. Data are the average of three replications $\pm$ SD.

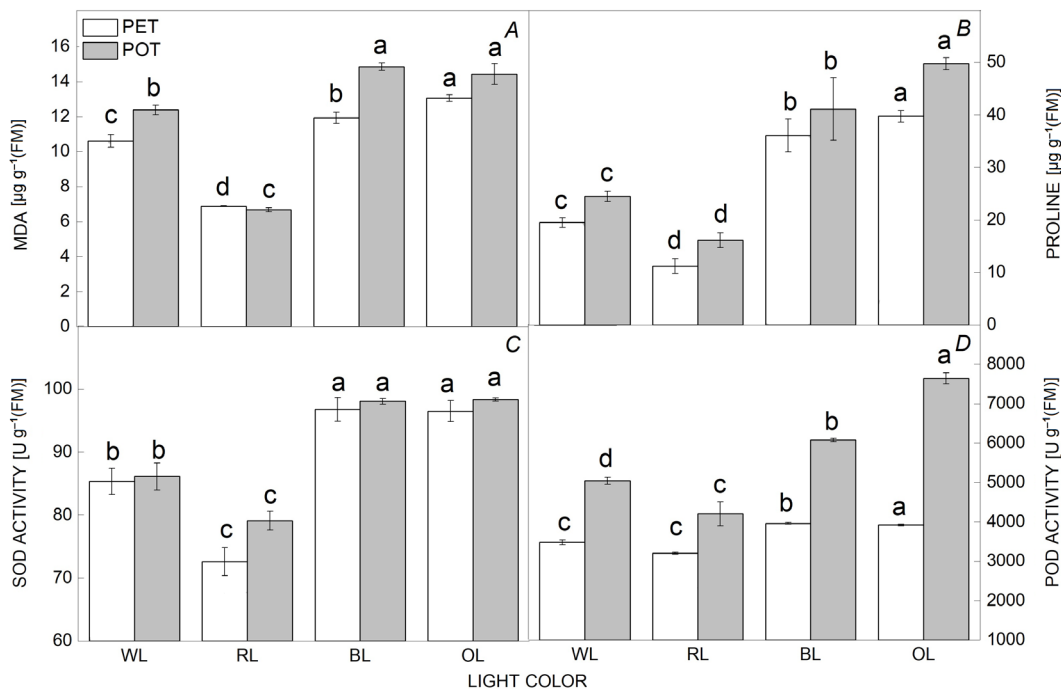


Fig. 4. Influence of different colors of light on malondialdehyde (MDA) (A), proline (B), superoxide dismutase (SOD) (C), and peroxidase (POD) (D) in *Brassica napus*. Relative radiance of plastic filter used: WL (white light), RL (red light), BL (blue light), and OL (orange light). Different letters indicate statistical differences ($P \leq 0.05$) or ($P \leq 0.01$) according to an LSD test. Data are the average of three replications $\pm$ SD. PET – Petri dish experiment; POT – pot experiment.

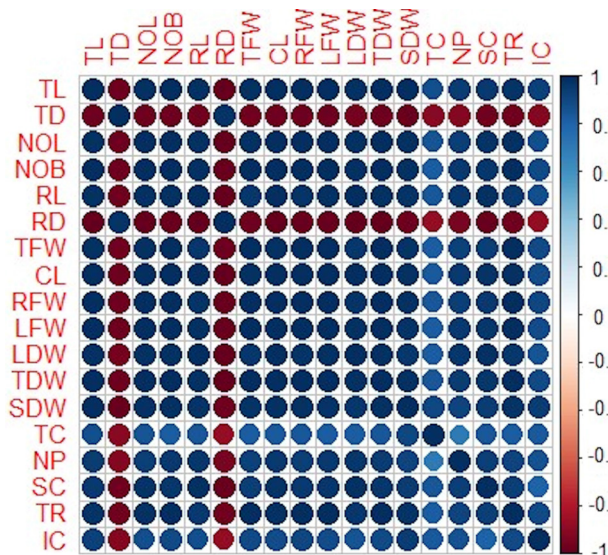


Fig. 5. Correlation of growth, chlorophyll, and gas-exchange parameters in *Brassica napus*. TL (plant height), TD (total plant diameter), NOL (number of leaves), NOB (number of branches), RL (root length), RD (root diameter), TFM (total fresh mass), CL (crown length), RFW (root fresh mass), LFM (leaf fresh mass), LDM (leaf dry mass), TDM (total dry mass), SDW (stem dry mass), TC (total chlorophyll content), P_N (net photosynthesis), g_s (stomatal conductance), E (transpiration rate), and C_i (intercellular CO_2).

Discussion

Light is an important component for the growth of plants besides water and oxygen. Various reports confirmed the morphological and physiological effects of light quality and the responses vary considerably depending upon plant species (Dutta Gupta and Jatothu 2013, Simlat *et al.* 2016). In our previous study, it was observed that RL increased plant height, biomass, and photosynthetic pigments, while reduced ROS production in the cell/tissues of *Corchorus capsularis* plants (Saleem *et al.* 2020b,d). In the present study, we investigated the effects of light quality (white, red, blue, and orange) on growth, photosynthesis, and ROS production of *B. napus* in order to determine the ideal light emission spectrum for optimal plant growth.

According to the results, we demonstrated that RL enhanced plant growth and biomass in *B. napus*, while BL and OL reduced plant growth and biomass when compared with WL (Tables 1–3). RL is considered as basal component in light spectra and normally considered as the best color of light among the light spectra for normal growth and development (Simlat *et al.* 2016, Yu *et al.* 2017). A previous study showed that different wavelengths of RL, *i.e.*, 660, 670, 680, and 690 nm promoted the growth and development in lettuce plants (Kim *et al.* 2004). RL wavelengths also encouraged stem growth, flowering, and fruit production. RL improves morphology (large and compact), higher biomass (fresh and dry mass) in Green oak and RL is an efficient source when Green oak was cultivated in hydroponic culture (Chen *et al.* 2014). In buckwheat sprouts, RL increased total biomass of the

plant along with leaf expansion and increase of phenolic compounds (Lee *et al.* 2014). In this study, plants grown under BL showed greater plant height but showed reduction in biomass and other morphological traits. Similar results were shown by Li *et al.* (2012). Hernández and Kubota (2016) proved that leaf area and dry matter increased up to 10% in cucumber seedlings when grown in BL. Godo *et al.* (2011) studied *Bletilla ochracea* seeds under OL and noticed that OL reduced seed germination, while OL induced formation of rhizoids. So these results suggest that RL promotes plant growth and biomass, while BL and OL reduce plant growth and biomass in comparison with WL. As a radiation-induced stress, BL and OL can decrease plant growth, while RL can increase growth and biomass.

In this study, changes in biomass accumulation in plants grown under varying light quality were closely linked to Chl contents and gas-exchange attributes. It has been revealed that RL plays a significant role in the photosynthetic apparatus development and affects morphogenesis by light-induced transformations of phytochrome system (Ma *et al.* 2015a). Light energy absorbed by Chl molecules can undergo three fates: (1) used to drive photosynthesis, (2) dissipated as heat (nonphotochemical quenching), or (3) reemitted as Chl fluorescence (Maxwell and Johnson 2000). Total Chl mainly comprises Chl *a* and Chl *b*, where Chl *a* is concentrated in photosystems and Chl *b* is the most abundant in LHC (Venema *et al.* 2000). Severe damage of photosynthetic pigments due to environmental stress causes reduction in Chl and carotenoid contents (Shao *et al.* 2014, Saleem *et al.* 2020a). RL significantly increased contents of Chl and carotenoids, whereas BL and OL resulted in their decrease (Fig. 2). The similar results were reported by Yu *et al.* (2017) who studied *Camptotheca acuminata* seedlings under different LEDs (WL, RL, BL, and YL) and noticed that the total contents of Chl and carotenoids decreased under BL and YL, while increased in RL in comparison with WL. They concluded that excess light, *i.e.*, BL and YL, may damage photosynthetic pigments in *C. acuminata* seedlings. Ma *et al.* (2015b) studied *Solanum tuberosum* under RL and BL and concluded that RL increased Chl and starch contents; they also noticed that RL improved plant growth and biomass in *S. tuberosum*. One more possible reason for the reduction of photosynthetic pigments in plants grown under BL and OL is the change in attributes of the electron transport chain (ETC) and organization in light harvesting which may cause a significant reduction in Chl and carotenoid contents in *B. napus* (Fan *et al.* 2013). Our results showed that RL increases P_N , g_s , E , and C_i , while BL and OL reduce these gas-exchange parameters (Fig. 3). Similar findings were shown by Yao *et al.* (2017) when they studied *B. napus* under the combination of BL and RL LEDs and noticed that composition of RL increases photosynthetic pigments in *B. napus* while BL reduces it. The similar results were also shown by Shimizu *et al.* (2011) in lettuce seedlings. The decline in gas-exchange parameters under BL and OL suggests a decrease in photosynthesis due to stomatal closure, therefore decreasing E and C_i (Hogewoning *et al.* 2007).

ROS can be generated by the direct transfer of the

excitation energy from Chl to produce singlet oxygen or by oxygen reduction in the Mehler reaction in the chloroplasts (Simlat *et al.* 2016, Saleem *et al.* 2020e) which promotes ROS accumulation, membrane lipid peroxidation, and disrupts the structure and function of cell membrane system (Rehman *et al.* 2019a, Saleem *et al.* 2020f). The ROS in plants are removed by a variety of antioxidant enzymes, such as SOD and POD. ROS, such as O_2^- , OH, and H_2O_2 , may oxidize proteins, lipids, and nucleic acids which results in abnormalities at the cellular level (Saleem *et al.* 2019d, Kamran *et al.* 2020b). The SOD catalyzes the dismutation of superoxide to H_2O_2 and molecular oxygen, whereas POD decomposes H_2O_2 by oxidation of co-substrates, such as phenolic compounds or antioxidants (Halliwell and Gutteridge 2007, Imran *et al.* 2019). In our study, plants under BL and OL not only had higher activities of SOD and POD, but also maintained higher amounts of MDA and proline than those under WL, indicating that oxidative damage to lipid membranes occurred in plants exposed to BL and OL (Fig. 4). To protect plants from harmful effects of ROS, antioxidant enzyme activity increased to reduce the accumulation of free radicals (Kamran *et al.* 2019, Khan *et al.* 2019, Rehman *et al.* 2019c). Plants exposed to the stress environment exhibited the accumulation of proline in their tissues (Fig. 4B). Accumulation of proline is an adaptive response of plants against stresses. Proline is believed to be regulatory or signal molecule activating some physiological and molecular responses (Szabados and Savouré 2010). In our study, increased SOD and POD activities were found in *B. napus* plants when exposed to BL and OL, whereas they were not shown in the RL treatment (Fig. 4C,D). Under BL, *Stevia rebaudiana* exhibited high activity of POD as reported by Simlat *et al.* (2016). Also, similar results were shown by Yu *et al.* (2017) for *C. acuminata* seedlings. The seedlings under BL showed the highest activities of SOD and POD while seedlings grown under RL showed low activities of antioxidant enzymes. These results depicted that plants grown under BL and OL showed high contents of MDA which means BL and OL caused oxidative damage to the leaves of *B. napus*. Though high proline accumulation in the leaves and high enzymatic activity of SOD and POD comes into play to minimize light stress induced by BL and OL.

On the basis of these findings, it can be concluded that RL promoted plant growth and development by increasing plant growth and biomass, photosynthetic pigments, gas-exchange parameters, and reducing ROS accumulation. On the other hand, BL and OL reduced plant growth and biomass by increasing the contents of MDA which means BL and OL induced oxidative damage in the leaves of *B. napus*. However, accumulation of high contents of proline and high enzymatic activities of SOD and POD in leaves of *B. napus* grown under BL and OL reduced the environmental stress. This study helped us investigate the response of *B. napus* to various light intensities and also the effects of these light sources on morphological, physiological, and other mechanisms of seedling and plants growth under different LEDs which can increase the seed yield of *B. napus* under greenhouse environment.

References

- Arnon D.T.: Copper enzyme in isolated chloroplasts. Polyphe-noloxidase in *Beta vulgaris*. – Plant Physiol. **24**: 1-15, 1949.
- Bates L.S., Waldren R.P., Teare I.D.: Rapid determination of free proline for water-stress studies. – Plant Soil **39**: 205-207, 1973.
- Bourget C.M.: An introduction to light-emitting diodes. – HortScience **43**: 1944-1946, 2008.
- Chang S., Li C., Yao X. *et al.*: Morphological, photosynthetic, and physiological responses of rapeseed leaf to different combinations of red and blue lights at the rosette stage. – Front. Plant Sci. **7**: 1144, 2016.
- Chen C.N., Pan S.M.: Assay of superoxide dismutase activity by combining electrophoresis and densitometry. – Bot. Bull. Acad. Sin. **37**: 107-111, 1996.
- Chen X.L., Guo W.Z., Xue X.Z. *et al.*: Growth and quality responses of 'Green Oak Leaf' lettuce as affected by monochromatic or mixed radiation provided by fluorescent lamp (FL) and light-emitting diode (LED). – Sci. Hortic.-Amsterdam **172**: 168-175, 2014.
- Cope K.R., Bugbee B.: Spectral effects of three types of white light-emitting diodes on plant growth and development: absolute versus relative amounts of blue. – HortScience **48**: 504-509, 2013.
- Dutta Gupta S., Jatothu B.: Fundamentals and applications of light emitting diodes (LEDs) in *in vitro* plant growth and morphogenesis. – Plant Biotechnol. Rep. **7**: 211-220, 2013.
- Evans P., Halliwell B.: Micronutrients: oxidant/antioxidant status. – Brit. J. Nutr. **85**: 67-74, 2001.
- Fahad S., Bajwa A.A., Nazir U. *et al.*: Crop production under drought and heat stress: Plant responses and management options. – Front. Plant Sci. **8**: 1147, 2017.
- Fahad S., Bano A.: Effect of salicylic acid on physiological and biochemical characterization of maize grown in saline area. – Pak. J. Bot. **44**: 1433-1438, 2012.
- Fahad S., Chen Y., Saud S. *et al.*: Ultraviolet radiation effect on photosynthetic pigments, biochemical attributes, antioxidant enzyme activity and hormonal contents of wheat. – J. Food Agric. Environ. **11**: 1635-1641, 2013.
- Fahad S., Hussain S., Bano A. *et al.*: Potential role of phytohormones and plant growth-promoting rhizobacteria in abiotic stresses: consequences for changing environment. – Environ. Sci. Pollut. R. **22**: 4907-4921, 2014a.
- Fahad S., Hussain S., Matloob A. *et al.*: Phytohormones and plant responses to salinity stress: a review. – Plant Growth Regul. **75**: 391-404, 2014b.
- Fahad S., Hussain S., Saud S. *et al.*: A biochar application protects rice pollen from high-temperature stress. – Plant Physiol. Bioch. **96**: 281-287, 2015a.
- Fahad S., Hussain S., Saud S. *et al.*: Exogenously applied plant growth regulators enhance the morphophysiological growth and yield of rice under high temperature. – Front. Plant Sci. **7**: 1250, 2016c.
- Fahad S., Hussain S., Saud S. *et al.*: Responses of rapid visco-analyzer profile and other rice grain qualities to exogenously applied plant growth regulators under high day and high night temperatures. – PLoS ONE **11**: e0159590, 2016a.
- Fahad S., Hussain S., Saud S. *et al.*: Exogenously applied plant growth regulators affect heat-stressed rice pollens. – J. Agron. Crop Sci. **202**: 139-150, 2016b.
- Fahad S., Hussain S., Saud S. *et al.*: Exogenously applied plant growth regulators enhance the morphophysiological growth and yield of rice under high temperature. – Front. Plant Sci. **7**: 1250, 2016c.
- Fahad S., Hussain S., Saud S. *et al.*: A combined application of

- biochar and phosphorus alleviates heat-induced adversities on physiological, agronomical and quality attributes of rice. – *Plant Physiol. Bioch.* **103**: 191-198, 2016d.
- Fahad S., Muhammad Z.I., Abdul K. *et al.*: Consequences of high temperature under changing climate optima for rice pollen characteristics – concepts and perspectives. – *Arch. Agron. Soil Sci.* **64**: 1473-1488, 2018.
- Fahad S., Nie L., Chen Y. *et al.*: Crop plant hormones and environmental stress. – *Sustain Agr. Rev.* **15**: 371-400, 2015b.
- Fan X.X., Xu Z.G., Liu X.Y. *et al.*: Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light. – *Sci. Hortic.-Amsterdam* **153**: 50-55, 2013.
- FAOSTAT: *Brassica napus*. Available at: <http://www.faostat.fao.org>, 2013.
- Fukuda N., Fujita M., Ohta Y. *et al.*: Directional blue light irradiation triggers epidermal cell elongation of abaxial side resulting in inhibition of leaf epinasty in geranium under red light condition. – *Sci. Hortic.-Amsterdam* **115**: 176-182, 2008.
- Godo T., Fujiwara K., Guan K., Miyoshi *et al.*: Effects of wavelength of LED-light on *in vitro* asymbiotic germination and seedling growth of *Bletilla ochracea* Schltr. (Orchidaceae). – *Plant Biotechnol.* **28**: 397-400, 2011.
- Haliapas S., Yupsanis T.A., Syros T.D. *et al.*: *Petunia × hybrida* during transition to flowering as affected by light intensity and quality treatments. – *Acta Physiol. Plant.* **30**: 807-815, 2008.
- Halliwell B., Gutteridge J.M.C.: *Free Radicals in Biology and Medicine*. Pp. 888. Oxford University Press, New York 2007.
- Heath R.L., Packer L.: Photoperoxidation in isolated chloroplasts. I. Kinetics and stoichiometry of fatty acid peroxidation. – *Arch. Biochem. Biophys.* **125**: 180-198, 1968.
- Hernández R., Kubota C.: Physiological responses of cucumber seedlings under different blue and red photon flux ratios using LEDs. – *Environ. Exp. Bot.* **12**: 66-74, 2016.
- Hogewoning S.W., Maljaars H., Harbinson J.: The acclimation of photosynthesis in cucumber leaves to different ratios of red and blue light. – *Photosynth. Res.* **91**: 287-288, 2007.
- Imran M., Sun X., Hussain S. *et al.*: Molybdenum-induced effects on nitrogen metabolism enzymes and elemental profile of winter wheat (*Triticum aestivum* L.) under different nitrogen sources. – *Int. J. Mol. Sci.* **20**: 3009, 2019.
- Janda T., Majláth I., Szalai G.: Interaction of temperature and light in the development of freezing tolerance in plants. – *J. Plant Growth Regul.* **30**: 460-469, 2014.
- Kami C., Lorrain S., Homitschek P., Fankhauser C.: Light regulated plant growth and development. – *Curr. Top. Dev. Biol.* **91**: 29-66, 2010.
- Kamran M., Malik Z., Parveen A. *et al.*: Biochar alleviates Cd phytotoxicity by minimizing bioavailability and oxidative stress in pak choi (*Brassica chinensis* L.) cultivated in Cd-polluted soil. – *J. Environ. Manage.* **250**: 109500, 2019.
- Kamran M., Malik Z., Parveen A. *et al.*: Ameliorative effects of biochar on rapeseed (*Brassica napus* L.) growth and heavy metal immobilization in soil irrigated with untreated wastewater. – *J. Plant Growth Regul.* **39**: 266-281, 2020a.
- Kamran M., Parveen A., Ahmar S. *et al.*: An overview of hazardous impacts of soil salinity in crops, tolerance mechanisms, and amelioration through selenium supplementation. – *Int. J. Mol. Sci.* **21**: 148, 2020b.
- Khan M.N., Zhang J., Luo T. *et al.*: Morpho-physiological and biochemical responses of tolerant and sensitive rapeseed cultivars to drought stress during early seedling growth stage. – *Acta Physiol. Plant.* **41**: 25, 2019.
- Kim S.J., Hahn E.J., Heo J.W., Paek K.Y.: Effects of LEDs on net photosynthetic rate, growth and leaf stomata of chrysanthemum plantlets *in vitro*. – *Sci. Hortic.-Amsterdam* **101**: 143-151, 2004.
- Kobayashi K., Amore T., Lazaro M.: Light-Emitting Diodes (LEDs) for miniature hydroponic lettuce. – *Opt. Photon. J.* **3**: 74-77, 2013.
- Lee S.C., Kim J.H., Jeong S.M. *et al.*: Effect of far-infrared radiation on the antioxidant activity of rice hulls. – *J. Agr. Food Chem.* **51**: 4400-4403, 2003.
- Lee S.W., Seo J.M., Lee M.K. *et al.*: Influence of different LED lamps on the production of phenolic compounds in common and Tartary buckwheat sprouts. – *Ind. Crop Prod.* **54**: 320-326, 2014.
- Li Z., Wu B.J., Lu G.Y. *et al.*: Differences in physiological responses of *Brassica napus* genotypes under water stress during seedling stage. – *Chin. J. Oil Crop Sci.* **34**: 033-039, 2012.
- Ma G., Zhang L., Kato M. *et al.*: Effect of the combination of ethylene and red LED light irradiation on carotenoid accumulation and carotenogenic gene expression in the flavedo of citrus fruit. – *Postharvest Biol. Tec.* **99**: 99-104, 2015b.
- Ma X.H., Song L.L., Yu W.W. *et al.*: Growth, physiological, and biochemical responses of *Camptotheca acuminata* seedlings to different light environments. – *Front. Plant Sci.* **6**: 321, 2015a.
- Mastropasqua L., Borraccino G., Bianco L., Paciolla C.: Light qualities and dose influence ascorbate pool size in detached oat leaves. – *Plant Sci.* **183**: 57-64, 2012.
- Maxwell K., Johnson G.N.: Chlorophyll fluorescence – a practical guide. – *J. Exp. Bot.* **51**: 659-668, 2000.
- Morrow R.C.: LED lighting in horticulture. – *HortScience* **43**: 1947-1950, 2008.
- Nanya K., Ishigami Y., Hikosaka S., Goto E.: Effects of blue and red light on stem elongation and flowering of tomato seedlings. – *Acta Hortic.* **956**: 261-266, 2012.
- Quartacci M.F., Ranier A., Sgherri C.: Antioxidative defense mechanisms in two grapevine (*Vitis vinifera* L.) cultivars grown under boron excess in the irrigation water. – *Vitis* **54**: 51-58, 2015.
- Rana M.S., Bhandana P., Sun X-C. *et al.*: Molybdenum as an essential element for crops: An overview. – *Int. J. Sci. Res. Growth* **24**: 2020.
- Rehman M., Liu L., Bashir S. *et al.*: Influence of rice straw biochar on growth, antioxidant capacity and copper uptake in ramie (*Boehmeria nivea* L.) grown as forage in aged copper-contaminated soil. – *Plant Physiol. Bioch.* **138**: 121-129, 2019a.
- Rehman M., Liu L., Wang Q. *et al.*: Copper environmental toxicology, recent advances, and future outlook: a review. – *Environ. Sci. Pollut. R.* **26**: 18003-18016, 2019b.
- Rehman M., Maqbool Z., Peng D., Liu L.: Morpho-physiological traits, antioxidant capacity and phytoextraction of copper by ramie (*Boehmeria nivea* L.) grown as fodder in copper-contaminated soil. – *Environ. Sci. Pollut. R.* **26**: 5851-5861, 2019c.
- Rehman M., Ullah S., Bao Y. *et al.*: Light-emitting diodes: whether an efficient source of light for indoor plants? – *Environ. Sci. Pollut. R.* **24**: 24743-24752, 2017.
- Rizwan M., Ali S., Adrees M. *et al.*: Cadmium stress in rice: toxic effects, tolerance mechanisms, and management: a critical review. – *Environ. Sci. Pollut. R.* **23**: 17859-17879, 2016.
- Sakharov I.Y., Aridilla G.B.: Variation of peroxidase activity in cacao beans during their ripening, fermentation and drying. – *Food Chem.* **65**: 51-54, 1999.
- Saleem M.H., Ali S., Rehman M. *et al.*: Influence of phosphorus on copper phytoextraction via modulating cellular organelles in two jute (*Corchorus capsularis* L.) varieties grown in a

- copper mining soil of Hubei Province, China. – *Chemosphere* **248**: 126032, 2020e.
- Saleem M.H., Ali S., Rehman M. *et al.*: Jute: A potential candidate for phytoremediation of metals – A review. – *Plants-Basel* **9**: 258, 2020f.
- Saleem M.H., Ali S., Seleiman M.F. *et al.*: Assessing the correlations between different traits in copper-sensitive and copper-resistant varieties of jute (*Corchorus capsularis* L.). – *Plants-Basel* **8**: 545, 2019a.
- Saleem M.H., Fahad S., Khan S.U. *et al.*: Copper-induced oxidative stress, initiation of antioxidants and phytoremediation potential of flax (*Linum usitatissimum* L.) seedlings grown under the mixing of two different soils of China. – *Environ. Sci. Pollut. R.* **27**: 5211-5221, 2020c.
- Saleem M.H., Fahad S., Khan S.U. *et al.*: Morpho-physiological traits, gaseous exchange attributes, and phytoremediation potential of jute (*Corchorus capsularis* L.) grown in different concentrations of copper-contaminated soil. – *Ecotox. Environ. Safe.* **189**: 109915, 2020d.
- Saleem M.H., Fahad S., Rehman M. *et al.*: Morpho-physiological traits, biochemical response and phytoextraction potential of short-term copper stress on kenaf (*Hibiscus cannabinus* L.) seedlings. – *PeerJ* **8**: e8321, 2020b.
- Saleem M.H., Kamran M., Zhou Y. *et al.*: Appraising growth, oxidative stress and copper phytoextraction potential of flax (*Linum usitatissimum* L.) grown in soil differentially spiked with copper. – *J. Environ. Manage.* **257**: 109994, 2020a.
- Saleem M.H., Rehman M., Zahid M. *et al.*: Morphological changes and antioxidative capacity of jute (*Corchorus capsularis*, Malvaceae) under different color light-emitting diodes. – *Braz. J. Bot.* **42**: 581-590, 2019b.
- Saud S., Chen Y., Fahad S. *et al.*: Silicate application increases the photosynthesis and its associated metabolic activities in Kentucky bluegrass under drought stress and post-drought recovery. – *Environ. Sci. Pollut. R.* **23**: 17647-17655, 2016.
- Saud S., Chen Y., Long B. *et al.*: The different impact on the growth of cool season turf grass under the various conditions on salinity and drought stress. – *Int. J. Agric. Sci. Res.* **3**: 77-84, 2017a.
- Saud S., Fahad S., Yajun C. *et al.*: Effects of nitrogen supply on water stress and recovery mechanisms in Kentucky bluegrass plants. – *Front. Plant Sci.* **8**: 983, 2017b.
- Saud S., Li X., Chen Y. *et al.*: Silicon application increases drought tolerance of Kentucky bluegrass by improving plant water relations and morphophysiological functions. – *Sci. World J.* **2014**: 368694, 2014.
- Sgherri C., Quartacci M.F., Navari-Izzo F.: Early production of activated oxygen species in root apoplast of wheat following copper excess. – *J. Plant Physiol.* **164**: 1152-1160, 2007.
- Shao Q.S., Wang H.Z., Guo H.P. *et al.*: Effects of shade treatments on photosynthetic characteristics, chloroplast ultrastructure, and physiology of *Anoectochilus roxburghii*. – *PLoS ONE* **9**: e85996, 2014.
- Shimizu H., Saito Y., Nakashima H. *et al.*: Light environment optimization for lettuce growth in plant factory. – *IFAC Proc. Vol.* **44**: 605-609, 2011.
- Simlat M., Ślęzak P., Mos M. *et al.*: The effect of light quality on seed germination, seedling growth and selected biochemical properties of *Stevia rebaudiana* Bertoni. – *Sci. Hortic.-Amsterdam* **211**: 295-304, 2016.
- Singh D., Basu C., Meinhardt-Wollweber M., Roth B.: LEDs for energy efficient greenhouse lighting. – *Renew. Sust. Energ. Rev.* **49**: 139-147, 2015.
- Sytar O., Zivcak M., Neugart S. *et al.*: Precultivation of young seedlings under different color shades modifies the accumulation of phenolic compounds in *Cichorium* leaves in later growth phases. – *Environ. Exp. Bot.* **165**: 30-38, 2019.
- Szabados L., Savaouré A.: Proline: a multifunctional amino acid. – *Trends Plant Sci.* **15**: 89-97, 2010.
- Thiyam-Holländer U., Aladedunye F., Logan A. *et al.*: Identification and quantification of canolol, sinapine and sinapic acid from Indian mustard oils and Canadian mustard products. – *Eur. J. Lipid Sci. Tech.* **116**: 1664-1674, 2014.
- Trouwborst G., Oosterkamp J., Hogewoning S.W. *et al.*: The responses of light interception, photosynthesis and fruit yield of cucumber to LED-lighting within the canopy. – *Physiol. Plantarum* **138**: 289-300, 2010.
- Urbanavičiūtė A., Pinho P., Samuolienė G. *et al.*: Effect of short wavelength light on lettuce growth and nutritional quality. Scientific Works of the Lithuanian Institute of Horticulture and Lithuanian University of Agriculture. Pp. 157-165. Lithuanian Institute of Horticulture and Lithuanian University of Agriculture, 2007.
- Venema J.H., Villerius L., van Hasselt P.R.: Effect of acclimation to suboptimal temperature on chilling-induced photodamage: Comparison between a domestic and a high-altitude wild *Lycopersicon* species. – *Plant Sci.* **152**: 153-163, 2000.
- Wang Y.C., Zhang H.X., Zhao B., Yuan X.F.: Improved growth of *Artemisia annua* L. hairy roots and artemisinin production under red light conditions. – *Biotechnol. Lett.* **23**: 1971-1973, 2001.
- Wu M.C., Hou C.Y., Jiang C.M. *et al.*: A novel approach of LED light radiation improves the antioxidant activity of pea seedling. – *Food Chem.* **101**: 1753-1758, 2007.
- Wu W., Ma B.L., Whalen J.K.: Enhancing rapeseed tolerance to heat and drought stresses in a changing climate: perspectives for stress adaptation from root system architecture. – *Adv. Agron.* **151**: 87-157, 2018.
- Yao X.Y., Liu X.Y., Xu Z.G., Jiao X.L.: Effects of light intensity on leaf microstructure and growth of rape seedlings cultivated under a combination of red and blue LEDs. – *J. Integr. Agr.* **16**: 97-105, 2017.
- Yu W., Liu Y., Song L. *et al.*: Effect of differential light quality on morphology, photosynthesis, and antioxidant enzyme activity in *Camptotheca acuminata* seedlings. – *J. Plant Growth Regul.* **36**: 148-160, 2017.
- Zhang J., Jiang F., Yang P. *et al.*: Responses of canola (*Brassica napus* L.) cultivars under contrasting temperature regimes during early seedling growth stage as revealed by multiple physiological criteria. – *Acta Physiol. Plant.* **37**: 7, 2015.
- Zhao X., Li Y.Y., Xiao H.L. *et al.*: Nitric oxide blocks blue light-induced K⁺ influx by elevating the cytosolic Ca²⁺ concentration in *Vicia faba* L. guard cells. – *J. Integr. Plant Biol.* **55**: 527-536, 2013a.
- Zhao X., Qiao X.R., Yuan J. *et al.*: Nitric oxide inhibits blue light-induced stomatal opening by regulating the K⁺ influx in guard cells. – *Plant Sci.* **184**: 29-35, 2012.
- Zhao X., Wang Y.L., Qiao X.R. *et al.*: Phototropins function in high-intensity blue light-induced hypocotyl phototropism in *Arabidopsis* by altering cytosolic calcium. – *Plant Physiol.* **162**: 1539-1551, 2013b.
- Zhao X., Zhao Q., Xu C. *et al.*: Phot2-regulated relocation of NPH3 mediates phototropic response to high-intensity blue light in *Arabidopsis thaliana*. – *J. Integr. Plant Biol.* **60**: 562-577, 2018.