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Growth characteristics and phytochemicals of canola (*Brassica napus*) grown under UV radiation and low root zone temperature in a controlled environment

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Abstract

We determined the effects of UV radiation and low root zone temperature on growth characteristics and phytochemicals of *Brassica napus* (canola) cultivated in a controlled environment (25/20 °C 16/8 [light/dark]; 70% relative humidity; 1000 $\mu\text{mol mol}^{-1}$ CO₂ with photosynthetic photon flux density of 100 and 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 7 and 18 days, respectively). The 18-day-old *B. napus* plants were treated for 5 days with two nutrient solution–temperature regimes (normal temperature [NT] and low-temperature [10 °C; LT]) and three levels of UV radiation (0, 0.3, and 0.6 W m⁻²). Treatment with 0.6 W m⁻² UV decreased quantum efficiency of photosystem II the most. Most growth characteristics decreased under LT + UV treatments. Treatments with 0.6 W m⁻² UV, compared to those without UV, significantly inhibited shoot height. LT + 0.3 and +0.6 UV decreased shoot height the most. Temperature (T) × UV interaction did not affect most growth characteristics except leaf area, specific leaf weight, and shoot water content. Antioxidant capacity (total ORAC) resembled lipophilic ORAC and showed the highest value in the LT + 0.6 UV treatment. T × UV interaction did not affect ORAC values, although LT + 0.3 UV and LT + 0.6 UV treatments produced the highest values. Both LT and UV radiation enhanced the total phenolic content, and in the combined treatments, it was two times that of the control. UV intensities (0.3 and 0.6 W m⁻²) remained constant regardless of variation in root zone temperature. UV radiation enhanced total flavonoid content equally across different intensities; LT + 0.6 W m⁻² UV treatment produced a relatively high value. Thus, LT and UV negatively affected plant growth parameters, except total dry weight, whereas LT, UV, or LT + UV positively affected antioxidant properties, total phenolics, and flavonoids, suggesting the potential of using an LT treatment in a hydroponic system as well as UV radiation to enhance growth performance of greenhouse and factory plants.

Keywords Antioxidant · Flavonoid · Hydroponic · Secondary metabolite · Total phenolic content

1 Introduction

Since the bioactive phytochemicals in *Brassicaceae* vegetables are a good source of antioxidants, *Brassica* species are becoming popular as staple foods worldwide (Jahangir et al. 2009a), including in China, Japan, India, and European

countries (Cartea et al. 2011). Among the *Brassicaceae* plants, *Brassica napus* L. (rapeseed or canola) has been generally grown as a primary source of oil, accounting for approximately 15% of global oil production (Fang et al. 2012). Meanwhile, *B. napus* leaves (vegetative canola tissues) also produce phytochemicals as antioxidant phenolics, including glucosinolates, phenylpropanoids, flavonoids, and phytoalexins (Font et al. 2005). In *B. napus*, these phytochemicals belong to a group of natural products and may be stimulated by and play important roles against biotic and abiotic stresses (Li et al. 2010).

During growth, plants may be exposed to various biotic and abiotic stresses. Abiotic factors such as water, light, temperature, and UV radiation are known to strongly affect primary and secondary metabolites in *Brassica* species (Jahangir et al. 2009a). Secondary metabolites, such as flavonoids,

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phenolics, terpenes, nitrogen-containing alkaloids, and sulfur-containing compounds, can be classified by their biosynthetic pathways (Crozier et al. 2006). Recently, environmental factors affecting edible *Brassicaceae* species high in secondary metabolites have been examined, and the antioxidant activity of such species has been investigated as a source of beneficial compounds in human diets (Cartea et al. 2011). Phenolics are among the most important groups of beneficial phytochemicals (Dixon and Paiva 1995), whereas flavonoids are the most widespread and diverse group of polyphenols in *Brassica* species (Cartea et al. 2011).

Among the various environmental factors exerting stress on the plants, low-temperature (LT) stress may induce the accumulation of secondary metabolites by reactive oxygen species (ROS) as a defense mechanism (Suzuki and Mittler 2006). Meanwhile, the effect of LT on the root zone of plants cultivated hydroponically has rarely been reported. Studies on the effects of root zone temperature (RZT) using a hydroponic system have been reported in various species, including *Spinacia oleracea* (spinach; Chadirin et al. 2011), *Lactuca sativa* (lettuce; He et al. 2009; Ilahi et al. 2017), *Solanum lycopersicum* (tomato; Adebooye et al. 2010), *Cucumis sativus* (cucumber; Yan et al. 2013), *Brassica oleracea* (broccoli; Díaz-Pérez 2009), and *Capsicum annuum* (bell pepper; Aidoo et al. 2017). However, there has been scarce research on the effects of RZT in *B. napus*. Previous studies that investigated the effects of RZT on *B. napus* have examined plant biomass, though the accumulation of phytochemicals has received little attention (Ye et al. 2003, 2006). For vegetables grown hydroponically in a controlled environment, environmental stress factors such as osmotic pressure, dissolved oxygen, and temperature can be easily regulated by manipulating the conditions of the nutrient solution in the root zone. Nonetheless, the accumulation of secondary metabolites affected by RZT remains largely unclear. Thus, the effect of RZT on the accumulation of phytochemicals should be further explored.

As an environmental stressor, UV radiation may damage plants and affect plant metabolites and nutritional qualities such as carbohydrates, organic and amino acids, vitamins, hormones, flavonoids, phenolics, and glucosinolates (Hounsome et al. 2008). In the UV range (280–400 nm), UV-B (280–315 nm) may impair plant growth and development. Enhanced levels of UV-B radiation inhibit plant physiological processes and growth (Day and Neale 2002). Meanwhile, UV-B can induce changes in the accumulation of antioxidants and secondary metabolites such as phenolic compounds, flavonoids, and hydroxycinnamic acids by increasing the levels of ROS (Jansen et al. 2008). Enhanced UV-B also affects the flavonoids and epicuticular wax as protective compounds in plants (Treutter 2005). Thus, the effects of UV radiation on plant secondary metabolites have recently been reviewed. Supplemental or full artificial lighting is

used in plant production systems such as in greenhouses and plant factories. UV radiation is especially important for the production of optimal-quality crops (Goto 2003).

Applying environmental stresses during cultivation is one method for manipulating the growth and bioactive compounds in plants. This is important for achieving more environmentally friendly agronomic practices and optimization of culture conditions. Previous studies have considered the effects of one factor (e.g., UV or LT) in plants; however, few studies have considered multiple factors such as UV-B and CO₂ (Qaderi and Reid 2005; Qaderi et al. 2007), temperature, and UV-B and water stress (Qaderi and Reid 2009; Qaderi et al. 2010). Meanwhile, significant interactions between the temperature and UV-B radiation have been observed, and the synergic effect on flavonoid concentration was more induced by LT and UV-B radiation (Martel and Qaderi 2016). León-Chan et al. (2017) also observed that LT with UV-B induce higher accumulation of phenolic compounds than each stress alone and detected specific flavonoids by LT and UV-B stress in bell pepper plants. On the basis of previous findings in other species, we hypothesized that both LT and UV radiation, during the cultivation of *B. napus*, affect the growth characteristics and accumulation of phytochemicals and that exposure to LT makes *B. napus* more vulnerable to the UV radiation effects on phytochemical accumulation than does exposure to normal RZT. However, there is limited information on the relationship between LT and UV radiation in *B. napus*. Therefore, multifactorial experiments are required to determine the plant growth responses as well as accumulation of bioactive compounds following environmental stress. The objective of this study was to investigate the interactive effects of LT and UV radiation on the growth characteristics and accumulation of phytochemicals in *B. napus*. Moreover, the results of the LT and UV radiation used in this study will provide information for their practical application in the greenhouse and plant factories.

2 Materials and methods

2.1 Plant materials and cultivation

One-day-old germinated *B. napus* seeds (*Brassica napus* L., ‘Kizakinonatané’; Noguchiseed, Saitama, Japan) were moved into a urethane sponge (M urethane, 2.3 × 2.3 × 2.7 cm, L × W × H; M Hydroponic Research Co., Aichi, Japan) and maintained in a plant factory under controlled environmental conditions (air temperature, average of 25/20 °C [16L/8D]; relative humidity [RH], 70%; CO₂ concentration, 1000 μmol mol⁻¹; photosynthetic photon flux density [PPFD] generated by fluorescent lamps [FL, FHF32EXNH; Panasonic Co., Osaka,

Japan], $100 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$; photoperiod, 16 h) for 7 d. *B. napus* seedlings were then transplanted into a cultivation panel (64-well normal type; M Hydroponic Research Co., Aichi, Japan) and cultivated using the deep flow technique (DFT) in a plastic container (32 plants per container; $55.5 \times 26 \times 14$ cm, L \times W \times H) under the same conditions used before transplanting without the light condition (PPFD, $200 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Table 1). A quarter strength of commercial nutrient solution (Otsuka Chemical Co., Osaka, Japan) was maintained a 6.4 pH, electrical conductivity (EC) value of 1.8 dS m^{-1} , and replaced every 3 d after transplanting.

2.2 LT and UV treatments

Eighteen days after sowing (DAS), *B. napus* plants were moved and grown on another shelf equipped with six treatments. LT and UV treatments consisted of two nutrient solution temperature regimes (normal temperature [NT] and low-temperature [10°C ; LT]) and three levels of UV radiation (0, 0.3, and 0.6 W m^{-2}), respectively: (1) NT with 0 W m^{-2} UV (control); (2) NT with 0.3 W m^{-2} ; (3) NT with 0.6 W m^{-2} ; (4) LT with 0 W m^{-2} UV; (5) LT with 0.3 W m^{-2} ; and (6) LT with 0.6 W m^{-2} . Inside of the shelves, environmental conditions were the same as those during the initial vegetative growth (see above). The low temperatures of the nutrient solution were maintained using a compact handy cooler (TRL-107NHF; Thomas Kagaku Co., Tokyo, Japan). The control was not kept in the cooler. During the treatment, the temperature of each nutrient solution was recorded by a data logger (GL820; Graphtec Co., Kanagawa, Japan) at 10-min intervals (Fig. 1). A specifically developed fluorescent lamp containing the UV spectrum (UV-FL) (FHF 32-EX-N-H; Panasonic Co., Osaka, Japan) was used for the UV treatments in this study. The spectral distribution and intensity were measured using a spectroradiometer (USR-45; USHIO INC., Yokohama, Japan) and UV radiometer (R203; Macam Photometrics Ltd., Livingston, UK), respectively (Fig. 2 and Table 2). At 18 DAS, the *B. napus* plants were subjected to each treatment for 5 d.

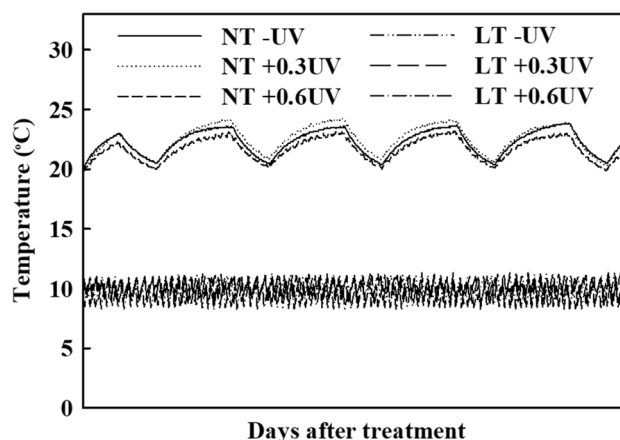


Fig. 1 Temperatures of the nutrient solutions during the treatment. Low temperature (10°C ; LT) with UV (0, 0.3, and 0.6 W m^{-2}) was controlled by a compact handy cooler before treatment. Data were collected with two thermocouple wires at each treatment

2.3 Growth characteristics

The heights of shoots and roots, fresh and dry weights of shoots and roots, leaf number, total leaf area, and specific leaf weight (SLW) were measured after the treatments. The heights and fresh weights of shoots and roots were measured with a ruler and an electronic scale (ASP2102; AS ONE Co., Osaka, Japan), respectively. The dry weights of shoots and roots were obtained by drying the sample for 74 h at 80°C in an oven (MOV-202F; Sanyo Electric Co., Osaka, Japan). The total leaf area was obtained from scanned leaf images using ImageJ software (Version 1.51 k; available online). Using leaf thickness, the SLW was calculated by dividing the milligrams of dry weight of shoots by the total leaf area. The water content was determined according to the equation:

$$\text{WC (\%)} = (\text{FW} - \text{DW}) / \text{FW} \times 100,$$

where FW represents fresh weight and DW represents dry weight of shoots or roots.

Table 1 Environmental conditions in a plant factory for *B. napus* plants during the experiment

Environmental factors	Stage		
	Seedling 0–7 DAS ^z	Vegetative 7–18 DAS	Treatment 18–23 DAS
Air temperature		25/20 $^\circ\text{C}$ (light/dark)	
Relative humidity		70%	
CO ₂ concentration		1000 $\mu\text{mol mol}^{-1}$	
PPFD ^y	$100 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$	$200 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$	
Photoperiod		16 h d ⁻¹	

^zDAS: Days after sowing

^yPPFD: Photosynthetic photon flux density

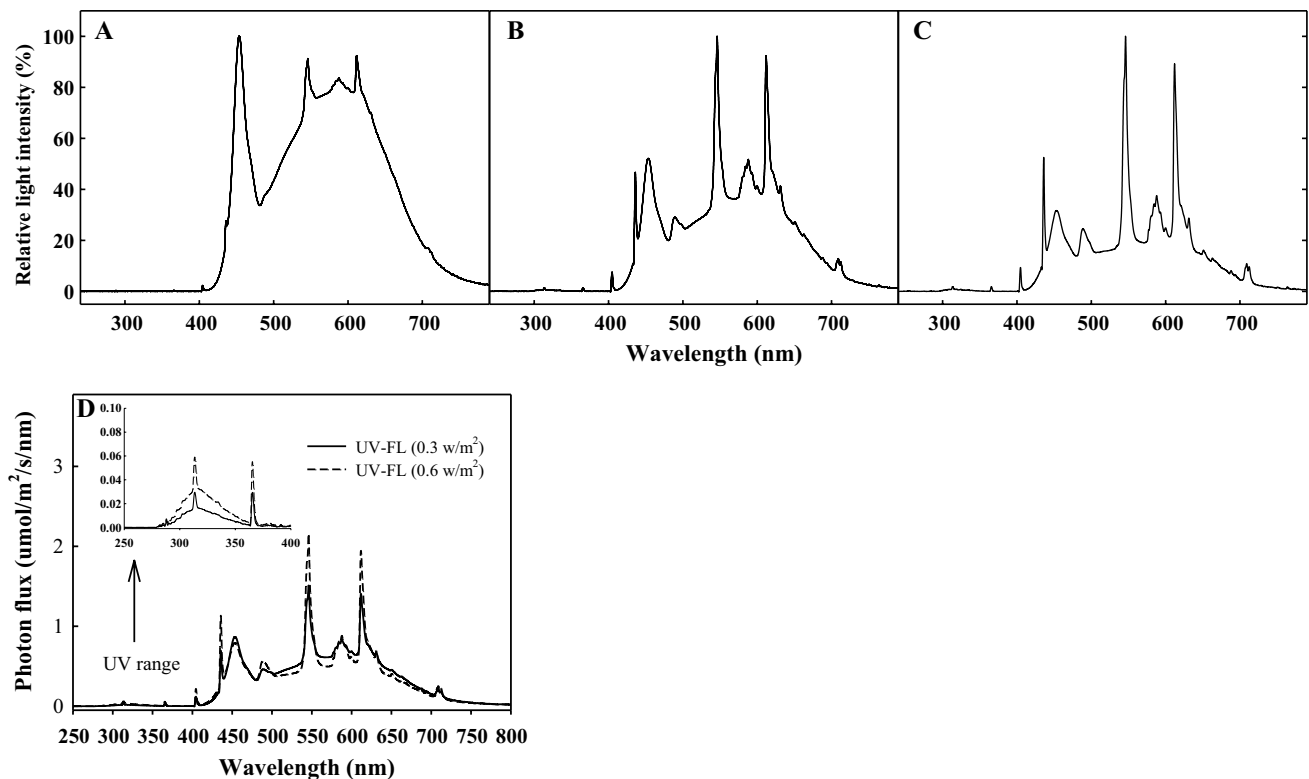


Fig. 2 Relative spectral distribution of lighting systems used in this study. Each light system consisted of white light-emitting diodes (W LEDs) and/or UV fluorescent lamp (UV-FL). W LEDs (**a**) (Control; 0 W m⁻² UV), W LEDs with 0.3 W m⁻² UV-FL (**b**), and W LEDs

with 0.6 W m⁻² UV-FL (**c**) were used in this study. The UV-FL lighting source emits UV and visible wavelengths (**d**). Total photosynthetic photon flux density (PPFD) was $200 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ in each treatment. Spectral scans were measured using a spectroradiometer

Table 2 Spectral characteristics of the UV treatment. Total photon flux densities were the same between the treatment

Parameter	Light source ^x		
	W LEDs (0 W m ⁻²)	W LEDs with UV-FL (0.3 W m ⁻²)	W LEDs with UV-FL (0.6 W m ⁻²)
Photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) ^z	200	200	200
UV (200–400 nm)	–	0.81	1.62
PAR (400– 700 nm)	200	199.19	198.38
Energy flux (W m ⁻²) ^y	–	0.3	0.6
UV-C (200– 280 nm)	–	0.08	0.16
UV-B (280– 315 nm)	–	0.08	0.16
UV-A (315– 400 nm)	–	0.14	0.28

^zPhoton flux density was measured using a spectroradiometer

^yEnergy flux was calculated from the spectral data

^xW LEDs: white light-emitting diodes, UV-FL: UV fluorescent lamps

2.4 Chlorophyll fluorescence

Chlorophyll (Chl) fluorescence was measured at the third leaf on the adaxial leaf surface with a portable Chl fluorescence meter (Mini-PAM; Walz, Effeltrich, Germany). Fluorescence readings were taken at 3, 4, and 5 d after treatment. The ratio of variable to maximal fluorescence (F_v/F_m) was measured in dark-adapted leaves that had been enclosed in cuvettes for 20 min. The saturating light pulse was delivered at $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 0.8 s.

2.5 Total phenolic content

The total phenolic content of leaves was extracted from the third leaf position within each treatment. Approximately 0.1 g (fresh tissue) of each third leaf from the bottom was extracted in 1.5 mL of 80% acetone and ground using an automatic grinder (Mixer Mill MM 200; Retch, Haan, Germany) at 30 Hz for 6 min. The extract was then incubated in darkness at 4 °C overnight. Subsequently, the extract was centrifuged at $20,500 \times g$ for 2 min, and the supernatant was used to measure the total phenolic concentration. The total phenolic content was determined using the modified

Folin-Ciocalteu reagent method (Ainsworth and Gillespie 2007). A mixture of 135 mL distilled water, 750 mL 1/10 dilution Folin-Ciocalteu reagent (Sigma-Aldrich, St. Louis, MO), and 600 mL 7.5% (w/v) Na_2CO_3 was added to 50 mL of the supernatant and vortexed for 10 s. The mixture was incubated at 45 °C in a water bath for 15 min and allowed to cool to room temperature (25 °C). The absorbance of the samples was read at 765 nm with a blank (50 mL of 80% [v/v] acetone) using a UV–VIS spectrophotometer (V-550, JASCO Co., Tokyo, Japan). The total phenolic content was expressed as milligrams gallic acid equivalent (GAE) per gram of dry weight of *B. napus* leaves.

2.6 Antioxidant capacity (ORAC)

Antioxidant capacity was determined using the ORAC assay following a modified method of Zhao et al. (2007). Recently, plant-derived compounds with antioxidant capacity and their involvement in human health have received much interest. Among the methods for examining antioxidant capacity in plants, the ORAC assay provides the advantage of direct measurement in both hydrophilic and lipophilic compartments (Prior 2015). Approximately 0.1 g (fresh tissue) of each third leaf from the bottom was extracted in 1 mL of 75 mmol L^{-1} phosphate buffer (pH 7.4) using a Mixer Mill MM 200 at 30 Hz for 6 min. The homogenate was then centrifuged at 20,500×g and 4 °C for 15 min. The supernatant was transferred to a microtube for use as the hydrophilic extract. The pellet was resuspended in 0.22 mL of acetone, vortexed for 5 s, and sonicated for 10 min. This acetone supernatant was used as the lipophilic extract. Briefly, 150 μL of 8.16×10^{-5} mmol L^{-1} fluorescein solution and 25 μL of phosphate buffer blank (75 mmol L^{-1} , pH 7.4) or 25 μL of Trolox standard (500, 250, 125, 62.5, 31.25, and 15.625 $\mu\text{mol L}^{-1}$) or 25 μL of diluted hydrophilic and lipophilic extraction were transferred to a 96-well plate. The well plate and 153 mmol L^{-1} 2, 2'-azobis (2-amidinopropane) dihydrochloride (AAPH) were immediately incubated at 37 °C for 30 min. Next, 25 μL of AAPH was added to each well. Fluorescence was measured using a microplate reader (SH-9000Lab; Corona Electric, Ibaraki, Japan) every 120 s at an emission and excitation wavelength of 520 and 485 nm, respectively. The ORAC values were expressed as mmol Trolox equivalents per dry mass (mM Trolox equivalents g^{-1} DW).

2.7 Total flavonoid content

The total flavonoid concentration was determined according to the method of Dewanto et al. (2002). Approximately 0.2 g (fresh tissue) of each third leaf from the bottom of the third leaf was extracted with 3 mL of 70% (v/v) ethanol (pH 3.2, using formic acid) and incubated overnight in the

dark at 4 °C. Subsequently, the extract was centrifuged at 20,500×g for 2 min, and the supernatant was used for total flavonoids. A mixture of 0.75 mL distilled water and 45 μL of 5% NaNO_2 was added to 150 μL of the extract. After 5 min, 90 μL of 10% AlCl_3 was added in the mixture and reacted for 6 min. Then, 300 μL of 1 M NaOH with 165 μL of distilled water was added to the mixture and reacted for 5 min. The absorbance of the mixture was measured at 510 nm after being vortexed for 10 s. The total flavonoid content was expressed as milligrams of (+)-catechin hydrate equivalents per gram of dry weight of *B. napus* leaves.

2.8 Statistical analyses

The experiment was repeated three times to verify the reproducibility of each experimental condition and time in a plant factory. All parameters were measured using four plants per treatment except for measurement of Chl fluorescent (three plants per treatment). Statistical analyses were conducted with Statistical Products and Service Solutions for Windows, ver. 24.0 (SPSS Inc., Chicago, IL, USA). Data were analyzed by two-way analysis of variance (ANOVA) to determine the interaction effect between UV radiation and temperature, and the differences between the means were tested using Duncan's multiple comparison test.

3 Results and discussion

3.1 Chlorophyll fluorescence

After dark acclimation, the maximum quantum efficiency of photosystem II (Fv/Fm) decreased in the treatments subjected to 0.6 W m^{-2} UV (NT or LT with +0.6UV) (Fig. 3). At 3 d after treatment, only the 0.6 W m^{-2} UV treatment had gradually decreased in Fv/Fm until 5 d after treatment. Although Fv/Fm in the combined treatment LT +0.6UV significantly decreased at 4 d after treatment, the Fv/Fm in the combined treatment LT +0.6UV slightly increased and had a value (0.784) similar to that of the control at 5 d after treatment.

The Fv/Fm value is a good indicator of photoinhibitory damage caused by light or other environmental stresses in plants (Maxwell and Johnson 2000). The reduction in Fv/Fm under UV radiation (0.6 W m^{-2}) at both NT and LT indicates that the PSII reaction center might have been damaged by UV radiation, which might have resulted in a lower quantum efficiency or photosynthetic capacity (Olsson et al. 2000). In accordance with our result that Fv/Fm was not affected by RZT, low and high RZT did not affect Fv/Fm in cucumber (Haghighi et al. 2015). Qaderi et al. (2007) also observed that *B. napus* leaves exposed to UV-B radiation at two levels of CO_2 concentration

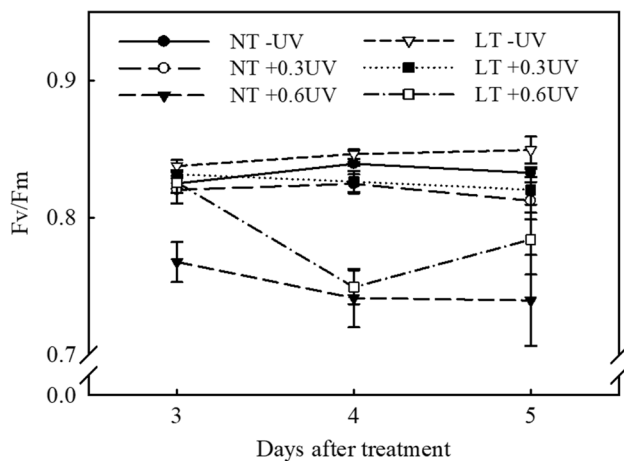


Fig. 3 Effect of different treatments on the maximum quantum efficiency of PSII (Fv/Fm) of *B. napus* leaves during the treatment. Bars represent standard errors ($n=3$). Different letters indicate significant differences according to Duncan's test ($p < 0.05$)

decreased Fv/Fm but had no effect on the two-way interaction between UV-B and CO_2 . This result is consistent with that of Moghadam et al. (2012), who observed that UV radiation had a stronger effect than water stress and CO_2 on Fv/Fm. As the energy of UV increased (UV-B doses; 8.5, 34, 68, 102 $\text{kJ m}^{-2} \text{day}^{-1}$), the Fv/Fm was decreased in *Ocimum basilicum* L. (sweet basil). In fact, UV radiation using high doses inhibit photosynthetic efficiency and increase in dissipation energy (Mosadegh et al. 2018). We observed that the Fv/Fm value did not decrease at 0.3 W m^{-2} UV radiation, suggesting that 0.3 W m^{-2} UV radiation did not affect PSII.

3.2 Growth characteristics

Overall, LT and UV radiation significantly influenced the growth characteristics (Tables 3, 4) of *B. napus*. Shoot height decreased as UV radiation increased. Meanwhile, treatments with 0.3 W m^{-2} UV radiation (NT +0.3UV and LT +0.3UV), regardless of nutrient solution temperature, did not significantly inhibit shoot height, relative to the treatments without UV radiation (NT -UV and LT -UV). However, treatments with 0.6 W m^{-2} UV radiation (NT +0.6UV and LT +0.6UV) did significantly inhibit shoot height compared with the treatments without UV radiation (NT -UV and LT -UV). LT, compared with NT, also inhibited shoot height, regardless of UV radiation. Combined treatments (LT +0.3UV and LT +0.6UV) yielded the lowest values in shoot height among all treatments. Root length was not significantly affected by nutrient solution temperature or UV radiation. The fresh weights of shoots and roots exhibited a similar trend with shoot height, which decreased as UV radiation or LT increased. The root fresh weight was more significantly affected by temperature than UV radiation, while there was no significant effect of UV radiation on root fresh weight. The dry weight of *B. napus* plants showed little difference between treatments except for the combined treatment with 0.6 W m^{-2} UV radiation (LT +0.6UV), which showed the greatest inhibition of dry matter (Table 3). Leaf number shared a similar trend with the dry weight of *B. napus* plants. Treatment with UV radiation or temperature as well as combined treatments significantly inhibited leaf area. Notably, leaf area was inhibited more by UV radiation than the nutrient solution temperature, which had a greater effect on shoot fresh weight. Leaf thickness (SLW) was increased by UV radiation and LT. The water

Table 3 Shoot height and root length, fresh and dry weights of shoot and root, and total dry weight for *B. napus* plants grown under UV and LT in a plant factory. Data were obtained after 5 days of treatment ($n=4-5$)

Factor ^z		Height/length (cm)		Fresh weight (g/plant)		Dry weight (g/plant)		Total dry weight (g/plant)
Temp.	UV (W m^{-2})	Shoot	Root	Shoot	Root	Shoot	Root	
NT	0	11.40 a ^y	21.70	13.96 a	3.30 ab	1.08 a	0.22 ab	1.30 a
	0.3	9.92 ab	23.52	10.34 bc	3.67 a	0.91 a	0.25 a	1.15 a
	0.6	8.70 bcd	21.66	10.82 b	3.81 a	0.99 a	0.26 a	1.24 a
LT	0	9.18 bc	23.02	8.11 cd	2.19 c	1.02 a	0.19 b	1.21 a
	0.3	7.56 cd	18.00	7.92 d	2.51 bc	0.93 a	0.22 ab	1.15 a
	0.6	7.06 d	18.56	6.25 d	1.95 c	0.70 b	0.18 b	0.88 b
Significance ^x								
Temp. (T)		***	NS	***	***	NS	**	*
UV		**	NS	*	NS	*	NS	NS
T × UV		NS	NS	NS	NS	NS	NS	NS

^zTreatment of temperature in nutrient solution and UV; NT (normal temperature), LT (low temperature; 10 °C), UV (0, 0.3, and 0.6 W m^{-2})

^yDifferent letters within columns indicate significant differences by Duncan at $p \leq 0.05$

^xNS indicates nonsignificant; *, **, *** significant at $p=0.05$, 0.01, and 0.001, respectively

Table 4 Leaf number, leaf area, SLW, and water content of shoot and root for *B. napus* plants grown under UV and LT in a plant factory. Data were obtained after 5 days of treatment (n = 4–5)

Temp.	Factor ^z	Leaf number per plant	Leaf area (cm ²)	SLW (mg cm ⁻²)	Water content (%)	
	UV (W m ⁻²)				Shoot	Root
NT	0	6.50	272.50 a ^y	3.95 c	92 a	93 a
	0.3	6.25	133.98 bc	6.87 ab	91 ab	93 a
	0.6	6.50	140.43 bc	7.08 a	91 b	93 a
LT	0	6.00	170.15 b	6.04 a	87 d	91 b
	0.3	6.00	145.53 bc	6.35 ab	88 cb	91 b
	0.6	6.00	104.43 c	6.73 ab	89 c	91 b
Significance ^x						
Temp. (T)		*	**	NS	***	***
UV		NS	***	***	NS	NS
T × UV		NS	**	**	**	NS

^zTreatment temperature in nutrient solution and UV; NT (normal temperature), LT (low temperature; 10 °C), UV (0, 0.3, and 0.6 W m⁻²)

^yDifferent letters within columns indicate significant differences by Duncan at $p \leq 0.05$

^xNS indicates nonsignificant; *****, significant at $p = 0.05$, 0.01, and 0.001, respectively

content of the shoots and roots was significantly decreased by LT. Except for leaf area, SLW, and shoot water content, there was no interactive effect of T × UV on the majority of *B. napus* growth characteristics (Table 4).

Reduced height in plants exposed to UV radiation implied that the specific photomorphogenic response of plants could be related to a UV-B photoreceptor by UV-B radiation (Lercari et al. 1990). Reduced plant height was also observed in *B. napus* (Qaderi and Reid 2005) and two other *Brassica* species (*B. rapa* and *B. nigra*) exposed to UV-B radiation (Conner and Zangori 1997). Meanwhile, root length showed no significant difference between treatments. RZT with LT enhanced root length in lettuce (He et al. 2009) but inhibited root length in cucumber seedlings (Yan et al. 2013) and a bell pepper cultivar (Aidoo et al. 2017). These results on the root morphology of RZT may affect the rate of water and nutrient intake (Domisch et al. 2001), functional activities of the root (Yan et al. 2013), and sensitivity of cells expanding in the root growth zone (Engels 1994). The results of these studies suggest that root physiological and morphological responses to UV or RZT may depend on the plant species. Most of the results demonstrate that various growth parameters were more inhibited by LT than by UV radiation. In general, plants sensitive to the effects of LT on the root system may respond quickly by restricting growth, but very little is known in this respect. The water content of shoots and roots decreased by LT might have partially restricted water uptake, which would inhibit photosynthesis and carbohydrate production (Table 4). The RZT affects the assimilate partitioning response in both shoot and root growth (Ye et al. 2006). Meanwhile, the dry mass of *B. napus* plants was little affected by LT (Table 3). Ye et al. (2003) reported that tropical species are more sensitive to LT than temperate species such as *B. napus* (oilseed rape).

Low RZT affects root cell membranes, increases water viscosity, and slows movement of water through roots (Kaufmann 1975), thus inhibiting plant growth through the reduced nutrient uptake and water content of plants, which was coincident with the current results. UV-B radiation can damage plants in many ways, impacting plant DNA (Britt et al. 1993), the photosynthetic apparatus (Greenberg et al. 1996), and plant growth (Day and Neale 2002). Qaderi et al. (2010) observed reductions in *B. napus* growth, such as in leaf number and area as well as plant dry mass by UV-B radiation. Gerhardt et al. (2008) also observed that UV treatment inhibited the morphology and growth of *B. napus* plants. The leaf area exposed to UV radiation in this study (Table 4) may be related to the UV-B-induced inhibition of cell expansion (Liu et al. 1995). The increased leaf thickness (SLW) due to UV radiation (Table 4) might act as a defense mechanism to prevent penetration into deeper tissues (Cen and Bornman 1993). Meanwhile, in some cases, UV-B radiation did not impair plant growth owing to increased tolerance or adaptation by the plants (Tevini 2000). Such findings are consistent with the present results that UV radiation did not affect the fresh and dry weight of roots, total dry weight, leaf number per plant, and water content (Tables 3, 4). This suggests that the UV radiation regimes used in this study were moderate in terms of plant dry mass production.

3.3 Antioxidant capacity (ORAC)

Hydrophilic ORAC was not significantly affected by UV radiation in both NT or LT, while LT significantly enhanced the hydrophilic ORAC up to two-fold (Table 5). Lipophilic ORAC was significantly increased by 0.6 W m⁻² UV radiation and LT treatments compared with that in the control. The total ORAC was similar to that of lipophilic ORAC

Table 5 Antioxidant capacity (ORAC) for *B. napus* plants grown under UV and LT in a plant factory. Data were obtained after 5 days of treatment (n=4)

Temp.	Factor ^z UV (W m ⁻²)	ORAC (mM Trolox equivalents g ⁻¹ DW)		
		Hydrophilic	Lipophilic	Total
NT	0	230.4 ± 86.4 c ^y	94.1 ± 62.3 b	324.6 ± 143.7 c
	0.3	340.9 ± 45.7 bc	194.0 ± 11.9 ab	534.8 ± 57.3 bc
	0.6	355.3 ± 87.9 bc	250.5 ± 41.0 a	605.7 ± 102.7 b
LT	0	483.1 ± 126.5 ab	215.4 ± 115.4 a	698.4 ± 237.3 ab
	0.3	462.1 ± 128.1 ab	254.1 ± 50.4 a	716.2 ± 178.2 ab
	0.6	561.2 ± 93.6 a	315.8 ± 118.1 a	877.0 ± 200.7 a
Significance ^x				
Temp. (T)		***	*	**
UV		NS	*	*
T × UV		NS	NS	NS

^zTreatment temperature in nutrient solution and UV; NT (normal temperature), LT (low temperature; 10 °C), UV (0, 0.3, and 0.6 W m⁻²)

^yMean ± standard deviation. Different letters within columns indicate significant differences by Duncan at $p \leq 0.05$

^xNS indicates nonsignificant; *****, significant at $p = 0.05$, 0.01, and 0.001, respectively

and showed the highest value in the LT +0.6UV combined treatment. The interaction between T × UV did not affect the ORAC values, although the combined treatments (LT +0.3 and 0.6UV) yielded the highest values.

Yan et al. (2013) observed the induced higher antioxidant enzyme activities caused by low RZT in cucumber seedlings. Moreover, LT stress in spinach roots induced antioxidation in shoots, which is applicable to the production of value-added leafy vegetables (Chadirin et al. 2011, 2012). These results on antioxidants and LT stress in the root system might influence secondary metabolism in plants. The ORAC values in this study may estimate two broad classes of antioxidants: hydrophilic compounds such as vitamin C and most polyphenolic antioxidants (phenolic acids, anthocyanins, and other flavonoids) and lipophilic antioxidants such as vitamin E and most carotenoids (Catoni et al. 2008). Interestingly, lipophilic ORAC had a significant effect on UV radiation ($p < 0.05$). In *Brassica* vegetables containing high levels of vitamins (e.g. carotenes and tocopherols), lipophilic phytochemicals such as tocopherols, sterols, and sterol esters also have important health-promoting properties (Jahangir et al. 2009b). The carotenoids exposed to UV radiation in *B. napus* plants presented no significant changes in previous studies (Olsson et al. 1999; Zhu and Yang 2015). Consistent with the results of the present study (data not shown), this finding implies that lipophilic phytochemicals other than carotenoids may play a more important role through UV radiation. Moreover, all ORAC values in the combined treatment with LT +0.6UV were the highest among all treatments, suggesting that the combination of LT and UV radiation may have a stronger effect on antioxidant capacity in *B. napus* than LT or UV radiation alone. Interactions of UV and other environmental conditions (light intensity, drought, or temperature) may stimulate the stress or affect the balance

between pro-oxidant production and scavenging capacity (Apel and Hirt 2004). Thus, environmental control of combination treatment must also be considered.

3.4 Total phenolic content

The total phenolic content was significantly affected by LT and UV radiation (Fig. 4). Both LT and UV radiation enhanced the total phenolic content, while, regardless of RZT, the different UV intensities (0.3 and 0.6 W m⁻²) had similar effects. Meanwhile, the total phenolic content of the combined treatments was the highest and increased up to two-fold compared with that in the control.

“Phenolic compound” is a generic term that refers to a large number of compounds (more than 8000). They are

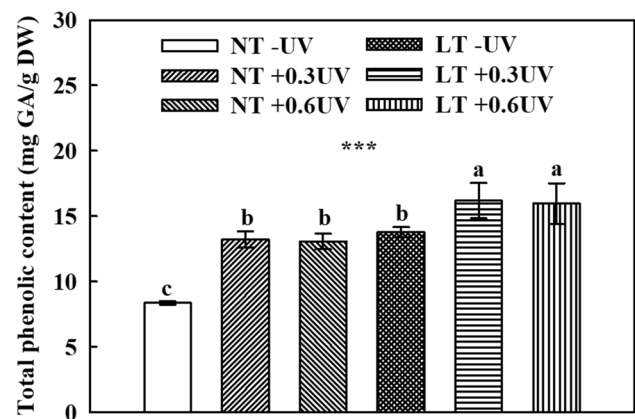


Fig. 4 Effect of different treatments on the total phenolic content of *B. napus* leaves during the treatment. Bars represent standard errors (n=4). Different letters indicate significant differences according to Duncan's test ($p < 0.05$)

widely dispersed throughout the plant kingdom and are produced in plants as secondary metabolites via the shikimic acid pathway (Cartea et al. 2011). Enhanced phenolic contents under LT and UV radiation in this study may stimulate the key enzyme of the phenylpropanoid metabolism, speeding up the biosynthesis of phenolic compounds (Luengo Escobar et al. 2017). In total phenolic content, similar patterns with ORAC values in combined treatments suggested that the combined effects of LT and UV radiation may have a stronger effect on phenolic acid in *B. napus* than LT or UV radiation alone. León-Chan et al. (2017) also observed that the combination of LT and UV-B induces higher accumulation of individual phenolic compounds than each stress alone. Lee et al. (2019) observed that a combined chilling and UV-A treatment (10 °C plus UV-A LED radiation at 30.3 W m⁻²) induced the total phenolic contents and phenylalanine ammonia-lyase activity in kale, compared to single (chilling or UV-A) treatments. They revealed that the carbon source could readily be distributed to secondary metabolite pathways under the combined chilling and UV-A treatment; therefore, two stressors might have synergetic effects on plants when applied simultaneously. Thus, our results suggested that plants exposed to LT stress are more susceptible to the direct damage of UV radiation because the plants induced more biosynthesis of UV-related compounds with a higher antioxidant capacity by LT to reduce the ROS produced in cells by the stress.

3.5 Total flavonoid content

Total flavonoid content was significantly affected by LT or UV (Fig. 5). UV radiation enhanced the total flavonoid content, while different UV intensities did not have significantly different effects (0.3 and 0.6 W m⁻²). The combined treatment with LT and 0.6 W m⁻² UV yielded a relatively high value. In contrast with total phenolic content and ORAC, sole LT (LT -UV) did not significantly affect the total flavonoid content compared with that in the control. The interactive effect on the total flavonoid content was observed only in the treatment with 0.6 W m⁻² UV radiation (NT +0.6UV vs. LT +0.6UV).

The higher total flavonoid content in the leaf suggests a higher nutritional value of leaves, as flavonoids possess strong antioxidant activity and inhibit oxidative stress (Pourcel et al. 2007). Our results are consistent with those of Olsson et al. (1998), who reported that *B. napus* subjected to UV-B showed a 70–150% increase in the overall flavonoid content (quercetin and kaempferol glucosides). Although many studies have reported an increase in flavonoids due to UV radiation in *B. napus*, the effect of flavonoids on the RZT is limited. In contrast with the results regarding ORAC and total phenolic content, LT did not affect flavonoids. This suggested that the flavonoids are more sensitive to UV

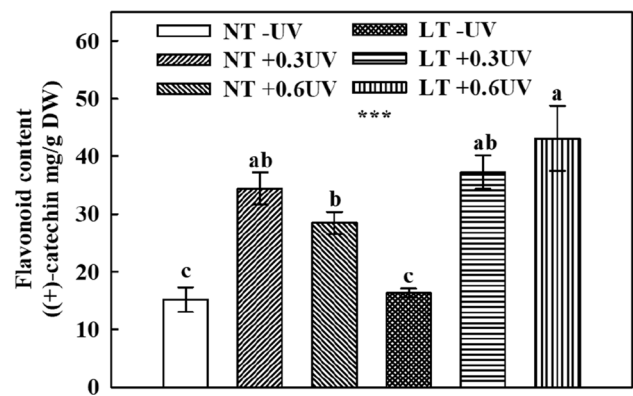


Fig. 5 Effect of different treatments on the flavonoid content of *B. napus* leaves during the treatment. Bars represent standard errors (n=4). Different letters indicate significant differences according to Duncan's test ($p < 0.05$)

radiation than they are to LT. León-Chan et al. (2017) also found that UV-B induces higher flavonoid synthesis than LT conditions. No significant differences in flavonoid levels were detected under chilling stress in kale (10 °C), but combined chilling and UV-A treatments led to significant increases in the levels of these compounds (Lee et al. 2019). Flavonoids are predominantly found in the epidermal cell, so they mainly absorb UV radiation to quench the ROS produced by UV stress (Castañeda-Ovando et al. 2009). In general, flavonoids, biosynthesized via the phenylpropanoid pathway, have a more important role in photoprotection against UV and free-radical scavengers than in other environmental conditions (Zoratti et al. 2014). As demonstrated in *B. napus*, the leaf epidermal layer produces flavonoids to protect the underlying tissues against UV-B radiation (Cen and Bornman 1993; Olsson et al. 1998). Meanwhile, further studies would be required to determine the synergetic effects of combined treatments with LT and UV radiation on flavonoids in *B. napus*.

4 Conclusion

In conclusion, this study revealed that RZT and UV radiation affect the growth and phytochemistry of *B. napus*. LT and UV radiation had negative effects on plant growth except for total dry weight, whereas LT, UV radiation, or combined treatment with LT and UV had positive effects on the antioxidant properties, total phenolics, and flavonoids of the plants. Even though LT did not influence the accumulation of flavonoids, the application of LT or UV radiation might have positively affected the antioxidant phenolic compounds without inhibiting dry biomass. Moreover, the combined treatment with LT and UV provided novel information to improve the quality of *B. napus*; however, a detailed study

on the synergetic effects under two environmental factors such as LT and UV should be considered. The results indicate the potential application of LT and UV radiation in a hydroponic system to induce antioxidant properties, phenolics, and flavonoids in the greenhouse and plant factory.

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Author contributions K-HS performed the experiments, collected the results and wrote the manuscript. MI participated in experiments and analysis the data. EG conceived made substantial contributions to the conception and design of the study. All authors have contributed significantly, and all authors are in agreement with the content of the manuscript.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

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