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# Growth of dropwort plants and their accumulation of bioactive compounds after exposure to UV lamp or LED irradiation

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## Abstract

High-energy ultraviolet (UV) light is an environmental stress that can be used to stimulate the biosynthesis of bioactive compounds in plants. This study aimed to comparatively determine the effects of UV-A, UV-B, and UV-C lamps or light-emitting diodes (LEDs) on the growth of dropwort (*Oenanthe stolonifera*) plants, and their contents of bioactive compounds. Dropwort seedlings with 2–3 offshoots were transplanted in a plant factory equipped with white LED and deep flow technique systems, and cultivated under standard growth conditions for 36 days. Thereafter, the dropwort plants were supplementally exposed to one of five UV treatments with energy equivalent to  $10 \text{ W m}^{-2}$ : UV-C lamps for 2 days, UV-B lamps for 3 days, and UV-A lamps and LEDs with 370 nm or 385 nm peak wavelengths for 14 days. The variable fluorescence (Fv) to maximum fluorescence (Fm) ratio (Fv/Fm) of dropwort leaves began to significantly decrease 3 h after exposure to UV-C, and 6 h after UV-B exposure. Fluorescence in UV-C and UV-B-treated plants was lower than in control and UV-A-treated plants during the entire period of UV irradiation. The fresh weight of the shoots of plants treated with UV was not significantly different to those of the control plants during the entire UV irradiation period. The total phenolic content of dropwort shoots exposed to UV-A and UV-B treatments significantly increased compared to that of the control 1 day after treatment. The total phenolic content was highest in plants treated with the 370 nm UV-A LED, and this was significantly higher (33%) than the control. Plants treated with the 385 nm UV-A LED on day 3 of treatment had the highest total phenolic content compared to the other treatments. A similar trend was observed in contents of flavonoids and persicarin. UV light induced higher anthocyanin content than the control. The activity of phenylalanine ammonia-lyase after UV treatments was significantly higher than the control, supporting the findings of our bioactive compound assays. In conclusion, the results of this study suggest that irradiating vegetables with UV-A LEDs would be useful in plant factories with artificial light for improving vegetable quality without inhibiting growth.

**Keywords** Anthocyanins · Chlorophyll fluorescence · Persicarin · Phenylalanine ammonia-lyase · Ultraviolet

## 1 Introduction

Dropwort (*Oenanthe stolonifera*, Umbelliferae) is a perennial, leafy stem vegetable with a unique aroma and flavor (Seo and Baek 2005). It also has superior nutritional value because of its high vitamin and mineral content (Hwang et al. 2011, 2013). In Asian countries, dropwort is commonly used as a folk medicine to treat jaundice, hypertension, diabetes, and abdominal pain, and as a food (Park et al. 1995; Ma et al. 2010). Dropwort contains numerous phenolic compounds such as caffeic acid, chlorogenic acid, and flavonoids. In particular, it contains the flavonoids persicarin and isorhamnetin, which are known to have hepatic

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detoxification and anti-inflammatory effects, to cure hanger, and prevent hypertension (Park et al. 2002; Yang et al. 2013).

There are two types of dropwort plants: water dropwort, which can be cultivated in paddy fields, and small dropwort, which can be cultivated in conventional fields. The reddish leaves and stems of small dropwort have stronger pharmacological activities than the greenish water dropwort leaves. For example, the antimutagenic and antioxidative effects of methanol extracts of small dropwort were higher than those of the water dropwort (Lee et al. 2004). Lee et al. (2001) also reported that the antibacterial activities of small dropwort grown under field conditions were higher than those of water dropwort. Thus, recently, the red-colored small dropwort has been commercialized for use in vegetable juices, kimchi, and herbal dressings. In addition, its utility has increased as a plant material for functional foods such as health-promoting beverages and dropwort pellets (Park et al. 1993; Son et al. 2005). Therefore, the development of optimal cultivation practices for improving the pharmacological quality of dropwort is required, but most previous studies have largely focused on improving crop production. Lee and Oh (2017) reported that, in small dropwort plants, the levels of antioxidant phenolic compounds and anthocyanins accumulated by water deficit during the growth stages.

The high-energy ultraviolet (UV) spectrum is divided into three ranges according to the wavelength: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (100–280 nm) (Wang et al. 2012). UV-A and UV-B constitute 98 and 1.5%, respectively, of the total UV radiation that reaches the Earth's surface. UV-C is completely absorbed by the stratospheric ozone layer and the atmosphere; therefore, it never reaches plants (Hollósy 2002; Lydie et al. 2016). High-energy UV irradiation generates reactive oxygen species (ROS) that damage DNA, RNA, proteins, chloroplasts, and photosynthetic pigments in plants (Hideg et al. 2013). Accordingly, UV radiation has a negative effect on the growth and development of plants (Nedunchezian and Kulandaivelu 1997; Frohnmeier and Staiger 2003; Singh et al. 2011; Lidon et al. 2012). In contrast, ROS generated in plants by benign UV treatments can act as signaling molecules (Pitzschke et al. 2006) and increase enzymatic and non-enzymatic antioxidants by activating gene expression and metabolism-related antioxidants as a defense mechanism in stressful conditions (Mackerness et al. 2001; Hideg et al. 2013). Non-enzymatic antioxidants include phenolic compounds such as flavonoids and vitamins. Red-colored anthocyanins are flavonoids that are generally known to accumulate in response to UV irradiation (Tsormpatzidis et al. 2008, 2010; Wang et al. 2012). Previous studies on UV irradiation have focused on investigating the effects of increased UV-B irradiation on plants because of concerns about destruction of the ozone layer (Vass et al. 2005). However, UV-B is

not suitable as a light source in plant cultivation because its high energy damages plant cells and DNA, as well as human cells and DNA. UV-A has relatively low energy compared to UV-B, is safe to handle, and has been reported to enhance plant growth (Xu and Gao 2010). Štroch et al. (2015) reported that the presence of UV-A mitigated or completely eliminated UV-B-induced damage to photosynthetic apparatus. However, it has been challenging to accurately determine the effect of UV-A on plants, because previous studies of UV-A have used lamps, which emit a broad range of wavelengths, even including visible light.

Thus, this study aimed to determine the effect of recently commercialized UV-A light-emitting diodes (LEDs) on the growth of dropwort plants and their contents of bioactive compounds compared to UV-A, UV-B, and UV-C lamps.

## 2 Materials and methods

### 2.1 Plant materials and cultivation conditions

Dropwort plantlets (average fresh weight  $2.9 \pm 0.1$  g) with 2–3 offshoots were transplanted into plastic pots ( $10.6 \times 10.6 \times 11.5$  cm, L  $\times$  W  $\times$  H, respectively) containing a growing medium (Myung-Moon; Dongbu Hannong, Seoul, Korea). Forty plantlets per UV treatment were placed on a culture bed of a plant factory ( $4 \times 2 \times 3$  m, L  $\times$  W  $\times$  H, respectively) equipped with white LEDs (Insungtech Co., Yongin, Korea), and were cultivated at an air temperature of 22 °C, with 60% relative humidity,  $650 \pm 50 \mu\text{mol mol}^{-1} \text{CO}_2$ , and  $270 \pm 5 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetic photon flux density (PPFD) on a 12 h light/dark period for 36 days. The plantlets were cultivated using deep flow technique (DFT) systems, and nutrient solution for dropwort [pH 6.5, electrical conductivity (EC)  $1.5 \text{ dS m}^{-1}$ ] (An and Lee 1991) was supplied immediately after transplantation and replaced at weekly intervals. The pH and EC of the nutrient solution were calibrated every 3 days using a digital multiparameter (Multi 3430; WTW, Weilheim, Germany).

### 2.2 UV treatments

Lighting systems of UV-A LEDs (LG Innotek, Seoul, Korea) with peaks at 370 nm and 385 nm were manufactured. UV-A (F20T10BLB), UV-B (G20T10E), and UV-C (G20T10, all Sankyo Ultraviolet, Tokyo, Japan) lamps, with peaks at 352 nm, 306 nm, and 254 nm, respectively, were compared with the UV-A LEDs. The energy intensities of UV treatments were measured using a spectroradiometer (JAZ-EL 200, Ocean Optics, Dunedin, FL, USA) at the position of dropwort leaves, and were equally set at  $10.6 \pm 0.2 \text{ W m}^{-2}$  from 12 points for each treatment because the maximum energy irradiated by UV-A lamps was about  $10 \text{ W m}^{-2}$ .

White LEDs were used as a control. The UV treatments consisted of supplemental UV lamps, or UV LEDs with white LEDs. The light spectral distributions of the white LEDs, UV lamps, and UV-A LEDs ranged from 190–890 nm by measuring 0.3-nm intervals using the spectroradiometer (Fig. 1). UV was irradiated continuously for 24 h per day, and the total irradiation periods were adjusted depending on the type of UV (2 days for UV-C lamps, 3 days for UV-B lamps, 14 days for UV-A lamps and LEDs of 370 nm and 385 nm), which were determined based on our previous study (Lee et al. 2014).

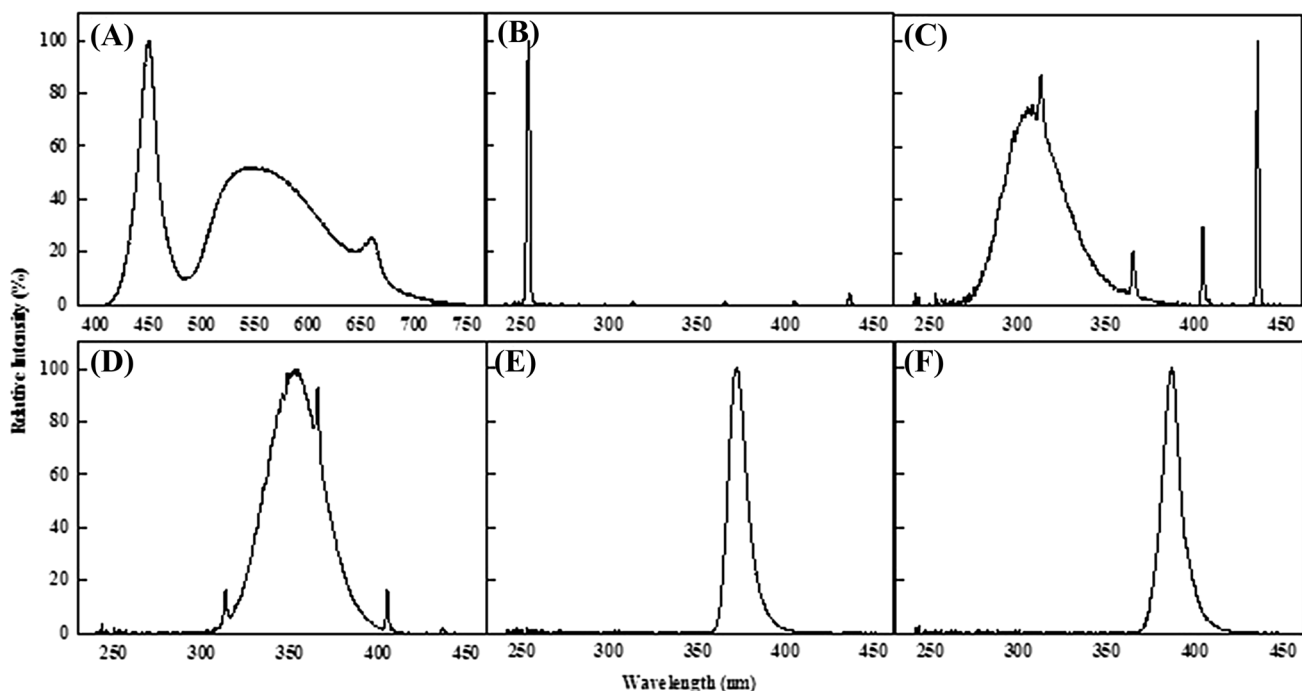
### 2.3 Chlorophyll fluorescence

The maximum quantum yield [variable fluorescence ( $F_v$ ) to maximum fluorescence ( $F_m$ ) ratio,  $F_v/F_m$ ] of photosystem II was analyzed to evaluate stress levels of dropwort leaves exposed to UV lamps or LEDs. Measurements were performed using a chlorophyll fluorescence meter (PAM 2000, Heinz Walz GmbH, Effeltrich, Germany) at 3-h intervals for the first 12 h, then at 6-h intervals for up to 3 days of treatment, and then at 12-h intervals from day 3–14 of UV treatment. The unfolded leaf of the stem growing on the second or third node was stabilized using a clip for 30 min in the dark before measurement, and the  $F_m$  and minimum fluorescence ( $F_0$ ) were obtained by

setting the total fluorescence ( $F_t$ ) value to approximately 0.2–0.3. The maximum quantum yield was calculated with the following equation:  $F_v/F_m = (F_m - F_0)/F_m$  (Maxwell and Johnson 2000).

### 2.4 Plant sampling and growth characteristics

Dropwort plants were sampled immediately before and during UV treatment. The samples were collected three times from each of the treated plants. Dropwort plants exposed to UV were sampled, and comparisons were made between the control and UV-A, UV-B, and UV-C-treated samples on day 1 of treatment, UV-B and UV-C on treatment day 2, UV-A and UV-B on day 3, and UV-A lamps and LEDs on day 14 of treatment (Table 1). To confirm the degree of growth disorder in dropwort plants exposed to UV, the shoot fresh and dry weights were measured. The fresh weight of the shoots was measured using an electronic scale (Si-234, Denver Instrument, Denver, CO, USA). Then, dropwort samples were freeze-dried for 72 h using a freezing dryer (PVTFD10A, ilShinBioBase, Dongducheon, Korea) at  $-50\text{ }^{\circ}\text{C}$  under a vacuum of 55 mmHg to measure the dry weight and analyze bioactive compounds.



**Fig. 1** Relative spectral distribution of white light-emitting diodes (LEDs) (a), ultraviolet (UV) lamps for UV-C (b), UV-B (c), and UV-A (d), and UV-A LEDs with peak wavelength at 370 nm (e) and 385 nm (f). Average photosynthetic photon flux density (PPFD) of all

light source was  $270 \pm 5\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ . Energy intensity of all UV treatments was equivalent to  $10.6 \pm 0.2\text{ W m}^{-2}$ . Spectral scans were measured at 23 cm from the lighting sources

**Table 1** Sampling dates of control and five ultraviolet (UV) treatments

Treatment	Before treatment	Days of UV treatment				
		0.4	1	2	3	14
Control	O	–	O	O	O	O
UV-C lamps	O	O	O	O	–	–
UV-B lamps	O	–	O	O	O	–
UV-A lamps	O	–	O	–	O	O
UV-A LEDs <sub>370</sub>	O	–	O	–	O	O
UV-A LEDs <sub>385</sub>	O	–	O	–	O	O

Each UV treatment was sampled total three times for comparison among UV-A, UV-B, and UV-C lamps (1 day), between UV-B and UV-C lamps (2 days), UV-A and UV-B (3 days), and UV-A lamps and UV-A light-emitting diodes (LEDs, 14 days,  $n=5$ )

## 2.5 Bioactive compounds

Freeze-dried shoot samples were ground at 15,000 rpm for 1 min using a grinder (Tube-Mill control, IKA, Wilmington, NC, USA), and the powders were stored at 4 °C until required for analysis.

### 2.5.1 Total phenolics

The total phenolic content of dropwort was determined using the Folin–Ciocalteu colorimetric method (Ainsworth and Gillespie 2007), with minor modifications. A powdered sample (40 mg) of dropwort shoots was mixed with 4 mL 80% (v/v) acetone. After sonication of the solution using an ultrasonic sonicator (SK5210HP, Hangzhou Nade Scientific Instrument Co., Ltd., Zhejiang, China) for 15 min, the resulting extract was stored in the dark at 4 °C overnight. Subsequently, the solution was centrifugated at  $3000 \times g$  for 2 min to separate the supernatant, which was used for analysis using the method described by Son and Oh (2013). The optical density of the final reaction solution was measured using a spectrophotometer (UV-1800, Shimadzu, Kyoto, Japan) at 765 nm to determine the total phenolic content, which was expressed as milligrams of gallic acid (Acros Organics, Geel, Belgium) equivalent per gram of dry weight (GAE mg g<sup>-1</sup> DW).

### 2.5.2 Total flavonoids

The total flavonoid content was determined according to the method described by Dewanto et al. (2002), with minor modifications. A powdered sample (40 mg) was mixed with 3 mL 70% (v/v) ethanol (pH 3.2, formic acid) and the solution incubated as described for the total phenolic analysis. Subsequently, the extract was separated by centrifugation at  $3000 \times g$  for 5 min, and the supernatant was analyzed. The supernatant (250 µL) was mixed with 1.25 mL distilled water and 75 µL 5% sodium nitrite (NaNO<sub>2</sub>). After 5 min, 150 µL 10% aluminum chloride (AlCl<sub>3</sub>) was added to the

mixture, and was allowed to react for 6 min. Thereafter, 500 µL 1 M sodium hydroxide (NaOH) and 275 µL distilled water were sequentially added to the mixture. After 5 min, the absorbance of the mixture was measured using a spectrophotometer (Shimadzu) at 510 nm. The total flavonoid content was expressed as (+)-catechin (mg) [(+)-catechin hydrate] (Sigma–Aldrich, St. Louis, MO, USA) equivalent per gram of dry weight (g DW) of dropwort shoots.

### 2.5.3 Persicarin

The persicarin content of dropwort was determined by chromatography and confirmed by comparing with the nuclear magnetic resonance (NMR) data reported by Kim et al. (2013). Each powdered sample (100 mg) was mixed with 1 mL 70% ethanol, and the solution was incubated for 2 h in an ultrasonication bath. The filtered extract (10 µL) was injected into a high-performance liquid chromatography (HPLC) system equipped with an Agilent series 1100 liquid chromatograph, G1322A vacuum degasser, G1310A quaternary pump, G1260 autosampler, G1329B column oven, and G1365 MWD detector (Agilent Technologies, Santa Clara, CA, USA). A YMC ODS-Pack A column (4.6 × 250 mm, 5 µm, YPC, Kyoto, Japan) was used to detect the persicarin content of the extract. The gradient profile was as follows: 0–10 min, 18% acetonitrile with 0.3% formic acid (A) and 82% water with 0.3% formic acid (B); 10–15 min, linear gradient 18–20% solvent A, 15–25 min, linear gradient 20–25% solvent A, and reconditioning steps to initial condition for 10 min. The flow rate was 1.0 mL min<sup>-1</sup> and 280 nm was used to detect persicarin. The stock solution with persicarin was diluted to a standard concentration range of 3.9063–1000 µg mL<sup>-1</sup> to construct the calibration curve.

### 2.5.4 Anthocyanins

Upper shoots, including the second or third node, were collected for qualitative and quantitative analysis of anthocyanins using the methods described by Wu et al. (2004)

and Choung (2008), with minor modifications. Samples (100 mg) ground after freeze-drying were mixed with 1 mL 80% methanol containing 0.5% hydrochloric acid (HCl) in a 2-mL microtube. The mixture was extracted using an ultrasonic sonicator (SK5210HP) for 1 h at 20 °C, and subsequently the supernatant centrifuged at  $3000 \times g$  for 10 min was transferred to a microtube. The procedure was repeated, and the additional supernatant was added to the amber microtube. The twice-extracted supernatant was filtered using a 0.22- $\mu\text{m}$  UHP (polytetrafluoroethylene, PTFE) syringe filter (SPU0213-1, Woongki, Seoul, Korea), and was collected in a 2-mL amber vial.

The HPLC system (YL9100, Young Lin Instrument Co., Ltd, Anyang, Korea) used for the analysis comprised a YL9101 vacuum degasser, YL9101 quaternary pump, YL9131 column compartment, YL9120 UV/visible (Vis) detector, and an autosampler. The Agilent Eclipse Plus-C18 column (4.6  $\times$  250 mm, 5  $\mu\text{m}$ , Agilent Technology, Santa Clara, CA, USA) was used to separate anthocyanins, and the mobile phase consisted of 5% formic acid (Sigma–Aldrich) in acetonitrile (Honeywell Burdick & Jackson, Morris Plains, NJ, USA, eluant A) and 5% formic acid in water (eluant B). The gradient profile of A was as follows: 10% (0 min), 10–20% (0–24 min), 20–80% (24–25 min), 80–60% (25–28 min), 60–10% (28–29 min), and 10% (29–38 min). The column temperature, sample injection volume, flow rate, and detection wavelength were 30 °C, 10  $\mu\text{L}$ , 0.8 mL  $\text{min}^{-1}$ , and 520 nm, respectively. Delphinidin 3-*O*- $\beta$ -D-glucoside (D3G), cyanidin 3-*O*-glucoside (C3G), and pelargonidin 3-*O*-glucoside (P3G; all Sigma–Aldrich) were used to construct the calibration curve. The anthocyanin content of dropwort was represented as micrograms per gram of dry weight ( $\mu\text{g g}^{-1}$  DW).

## 2.6 PAL activity

The activity of PAL, a key gateway enzyme in the biosynthetic pathway of secondary metabolites, was expressed as

the content of *trans*-cinnamic acid generated by L-phenylalanine (Boo et al. 2011). Leaves in the stems at the second or third node from the top (approximately 1 g) were sampled and stored at  $-70$  °C in a deep freezer until required for analysis. After the frozen samples were ground with liquid nitrogen in a mortar, the powder was extracted with 10 mL 25 mM borate buffer (pH 8.8) and 2 mL 3 mM  $\beta$ -mercaptoethanol. Subsequently, the extract was centrifuged at  $3000 \times g$  for 20 min, and the supernatant was analyzed. The supernatant (5 mL) was mixed with 2.5 mL each of 25 mM borate buffer (pH 8.8) and 10 mM L-phenylalanine, and reacted in a water bath at 40 °C for 2 h. The reaction was stopped with 100  $\mu\text{L}$  5 N HCl, and the optical density of the reaction solution was measured using a spectrophotometer (Shimadzu) at 290 nm. The PAL activity of dropwort leaves was represented as millimoles of *trans*-cinnamic acid equivalent per hour per gram of fresh weight ( $\text{mM trans-cinnamic acid h}^{-1} \text{g}^{-1} \text{FW}$ ).

## 2.7 Statistical analysis

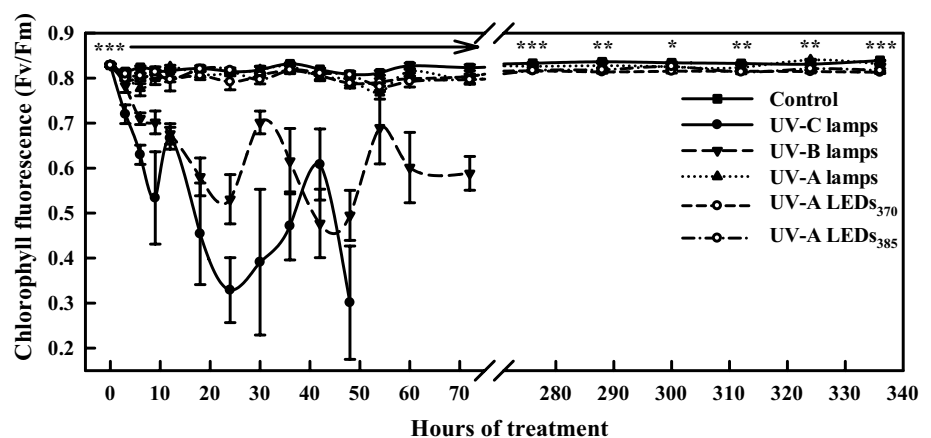
Five replicates were used for each measurement parameter, except for the  $F_v/F_m$ , which had four replicates. The SAS software program (SAS 9.2, SAS Institute Inc., Cary, NC, USA) was used for statistical analysis. One-way analysis of variance (ANOVA) was conducted, and the significant difference between the means of treatment groups was compared using Duncan's multiple range test.

## 3 Results

### 3.1 Chlorophyll fluorescence

The  $F_v/F_m$  was measured to confirm stress levels of dropwort plants subjected to UV irradiation (Fig. 2). Different trends in the changes in  $F_v/F_m$  were observed depending on the wavelength of UV treatment. Compared to those of

**Fig. 2** Chlorophyll fluorescence [variable fluorescence ( $F_v$ ) to maximum fluorescence ( $F_m$ )] ratio ( $F_v/F_m$ ) of dropwort plants continuously exposed to ultraviolet (UV)-C lamps for 2 days, UV-B lamps for 3 days, and UV-A lamps and light-emitting diodes (LEDs) for 14 days. The vertical bars indicate standard errors ( $n=4$ ). \*\* and \*\*\* represent significant differences at  $p < 0.01$  and  $p < 0.001$ , respectively





the control, the  $F_v/F_m$  values of dropwort leaves exposed to UV-C started to significantly decrease after 3 h of UV irradiation, and for UV-B lamps after 6 h. In case of plants treated with UV-A (UV-A lamps and both UV-A LEDs), the  $F_v/F_m$  values were significantly lower than those of the control after 72 h (3 days) to 336 h (14 days) of UV irradiation, although the values were maintained above 0.8 during the entire period.

### 3.2 Growth characteristics

There were no significant differences in shoot fresh weight between control plants and those in any of the UV-treated conditions throughout the irradiation period (Table 2). Dropwort plants exposed to UV-C or UV-B lamps suffered from physiological disorders at the end of the irradiation period, therefore they did not exhibit growth characteristics. Treatment with UV-A, whether by lamp or LEDs, appeared to have no negative effect on shoot growth during the irradiation period.

### 3.3 Total phenolic, total flavonoid, and persicarin content

The total phenolic content, total flavonoid content, and persicarin content were measured in dropwort plants continuously exposed to UV-C lamps for 2 days, UV-B lamps for 3 days, and UV-A lamps and LEDs for 14 days (Fig. 3). The total phenolic content of the shoots of dropwort plants exposed to UV-A and UV-B significantly increased compared to the control on day 1 of UV treatment (Fig. 3a). In particular, the total phenolic content of plants treated with the 370-nm UV-A LED was 33% higher than that of the control plants, and was the highest among all UV treatments. On day 2 of UV treatment, no positive increase in bioactive compounds was observed in plants treated with UV-B or UV-C lamps.

Plants treated with the 385-nm UV-A LEDs had the highest total phenolic content on days 3 and 4 of treatment compared to the control and other UV treatments, although this difference was not significant. Plants in all UV treatment conditions exhibited a trend of increasing total phenolic content with increasing UV irradiation period.

The total flavonoid content exhibited a similar trend to that of total phenolic content during the UV treatment period (Fig. 3b). The effect of wavelength on persicarin content was clear, unlike the contents of total phenolics and flavonoids, although all UV treatments were administered at the same energy level of  $10.6 \text{ W m}^{-2}$  (Fig. 3c). One day of treatment with UV-A and UV-B induced higher persicarin content than was observed in the control plants on day 1. Compared to control plants, persicarin content was 1.8 times higher in plants treated with the UV-A lamps, and 2.1 times higher in those treated with the 370-nm UV-A LEDs. On day 3 of UV treatment, the 385-nm UV-A LEDs induced 3.7 times more persicarin than in plants treated with the UV-B lamps, and 1.9 times more than in plants treated with 370-nm UV-A LEDs. In plants treated with UV-A lamps and 370-nm LEDs, the persicarin content decreased on day 3, unlike those on day 1 of UV treatment, and this was significantly lower than the control. On day 14 of UV treatment, the difference in persicarin content between the control and UV-A-treated plants was not significant.

### 3.4 Anthocyanin content

The leaves and stems of dropwort plants exposed to UV lamps or UV LEDs were more red in color than those of the control plants (Fig. 4a, b). Three types of anthocyanins, D3G, C3G, and P3G, were identified in dropwort shoots. All dropwort plants exposed to UV irradiation accumulated higher levels of anthocyanins than the control plants during the irradiation period (Fig. 4c). On day

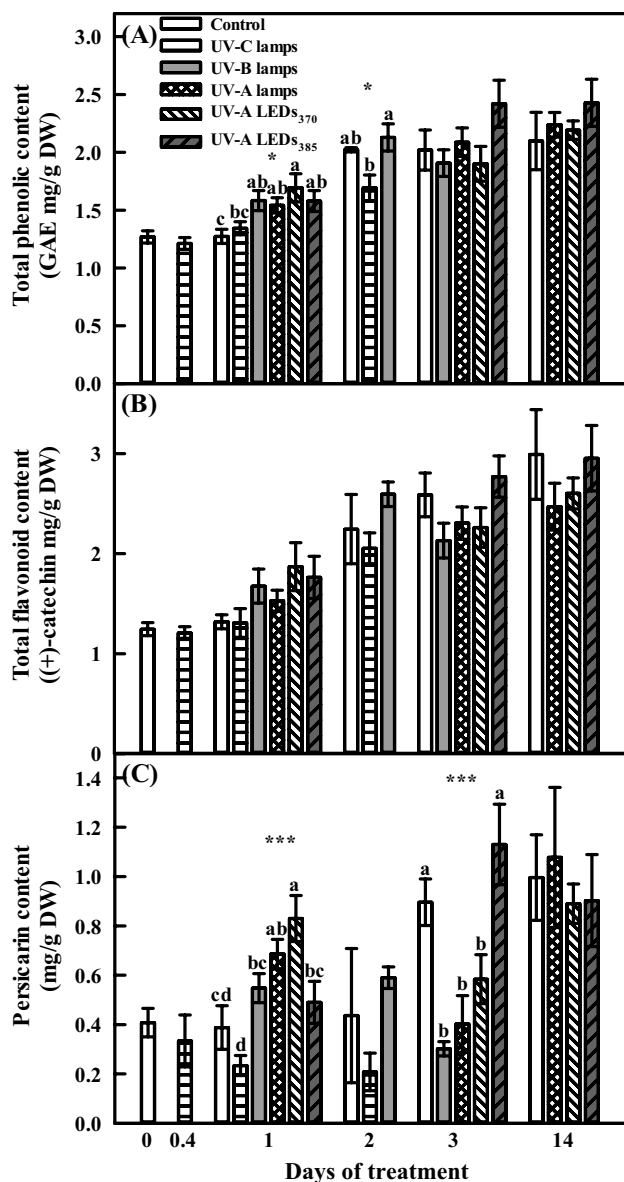
**Table 2** Shoot fresh weight of dropwort plants continuously subjected to ultraviolet (UV)-C lamps for 2 days, UV-B lamps for 3 days, and UV-A lamps, and light-emitting diodes (LEDs) for 14 days

Light source	Shoot fresh weight (g/plant)					
	Before treatment	Days of treatment				
		0.4	1	2	3	14
Control <sup>z</sup>	46.9 ± 6.0	–	44.8 ± 7.7 <sup>y</sup>	54.8 ± 5.1	64.2 ± 13.9	105.9 ± 17.4
UV-C lamps		40.7 ± 7.4	43.1 ± 8.1	54.8 ± 6.7	–	–
UV-B lamps		–	51.6 ± 9.8	49.5 ± 2.2	59.8 ± 4.8	–
UV-A lamps		–	48.0 ± 3.4	–	80.5 ± 6.7	83.9 ± 13.5
UV-A LEDs <sub>370</sub>		–	41.9 ± 7.0	–	69.2 ± 11.4	95.5 ± 15.3
UV-A LEDs <sub>385</sub>		–	48.5 ± 6.1	–	66.8 ± 16.9	106.7 ± 11.5
Significance <sup>x</sup>			NS	NS	NS	NS

<sup>z</sup>Control: white LEDs (450 nm, 27% + 555 nm, 65% + 660 nm, 8%), n = 5

<sup>y</sup>Data are shown as mean ± standard error

<sup>x</sup>NS nonsignificant



**Fig. 3** Content of total phenolics (a), total flavonoids (b), and persicarin (c) of dropwort plants exposed to ultraviolet (UV) lamps or UV light-emitting diodes (LEDs). Vertical bars indicate standard errors. Statistically significant differences are indicated at \* $p < 0.05$  and \*\*\* $p < 0.001$  ( $n = 5$ )

1 of UV treatment, plants treated with UV-C lamps had an anthocyanin content that was two-fold higher than controls, and those treated with UV-B lamps had 2.1 times more anthocyanin. The average anthocyanin content of dropwort plants exposed to UV irradiation was 2.4 times higher than the control plants, except for the plants treated with the 370-nm UV-A LEDs on day 3 of UV treatment. Both types of UV-A treatment (UV-A lamps and LEDs) induced the accumulation of anthocyanins, especially of C3G, by day 14 of UV treatment.

### 3.5 PAL activity

PAL activity was measured in plants treated with UV-C and UV-B lamps for 3 days (Fig. 5a) and in plants treated with UV-A lamps and LEDs for 14 days (Fig. 5b). On day 1 of UV treatment, plants grown under UV-C lamps reached their highest levels of enzyme activity; in fact, after just 0.4 days of UV treatment, the enzyme activity of these plants was significantly higher (by 32%) than in the control plants. The PAL activity of UV-B lamp-treated plants gradually increased with increasing irradiation period, and was highest on day 3 of UV treatment; this was significantly higher (36%) than in control plants. The PAL activity of plants treated with UV-A lamps and 385-nm UV-A LEDs was significantly higher than control plants on day 3 of UV treatment. On day 14 of the treatment, plants in all UV-A-treated conditions had significantly higher PAL activity than in controls. The activity of PAL in plants treated with UV-A lamps, however, decreased on day 14 of treatment, while the activity of PAL in plants treated with UV-A LEDs continued to increase. Exposure to 385-nm UV-A LEDs induced the highest PAL activity among UV-A treatments regardless of the irradiation period; these values were significantly higher (55%) than those of the control on day 14 of UV treatment.

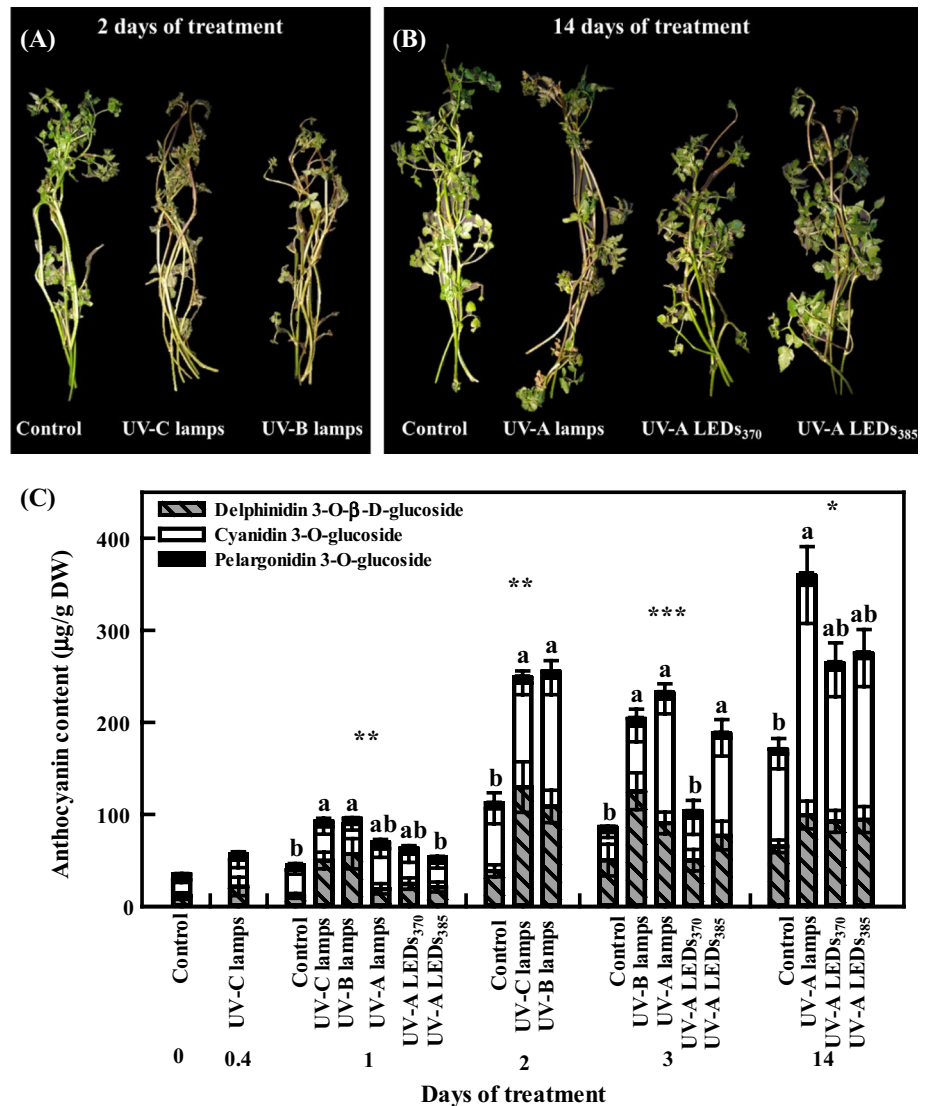
## 4 Discussion

### 4.1 Chlorophyll fluorescence

The chlorophyll fluorescence value ( $F_v/F_m$ ) indicates the photosynthetic performance of plants using nondestructive measurement, and represents the maximum photochemical efficiency of the reaction center of photosystem II (PS II). The  $F_v/F_m$  of plants grown under normal growth conditions is generally in the range 0.8–0.84, indicating efficient light utilization for photosynthesis (Maxwell and Johnson 2000; Fu et al. 2012). However,  $F_v/F_m$  decreases in response to abiotic stresses such as low temperature, high light intensity, and UV irradiation. Thus, the value has been used as a stress indicator (Groom and Baker 1992). In the present study, UV stress decreased  $F_v/F_m$  (Fig. 2). We assume this is a result of a UV irradiation-induced decrease in PS II activation, which damages D1 and D2 proteins of the PS II reaction center (Vass et al. 2005; Sicora et al. 2006). These effects subsequently impede the biosynthesis of chlorophyll a and b, and their combination with proteins of the light-harvesting complex of PSII (LCHII) (Jordan et al. 1991, 1994). When lettuces were irradiated by UV-A, UV-B, and UV-C lamps, it was revealed that UV-C has high energy because of its short wavelength. Therefore, compared to treatment with UV-B or UV-A lamps, UV-C there was a greater decrease  $F_v/F_m$  (Lee et al. 2014). A similar trend was observed in the



**Fig. 4** Shoot color change on day 3 (a) and 14 (b) of ultraviolet (UV) treatment and anthocyanins content (c) of dropwort plants exposed to UV lamps or UV light-emitting diodes (LEDs). Statistically significant differences are indicated at \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$  ( $n = 5$ )

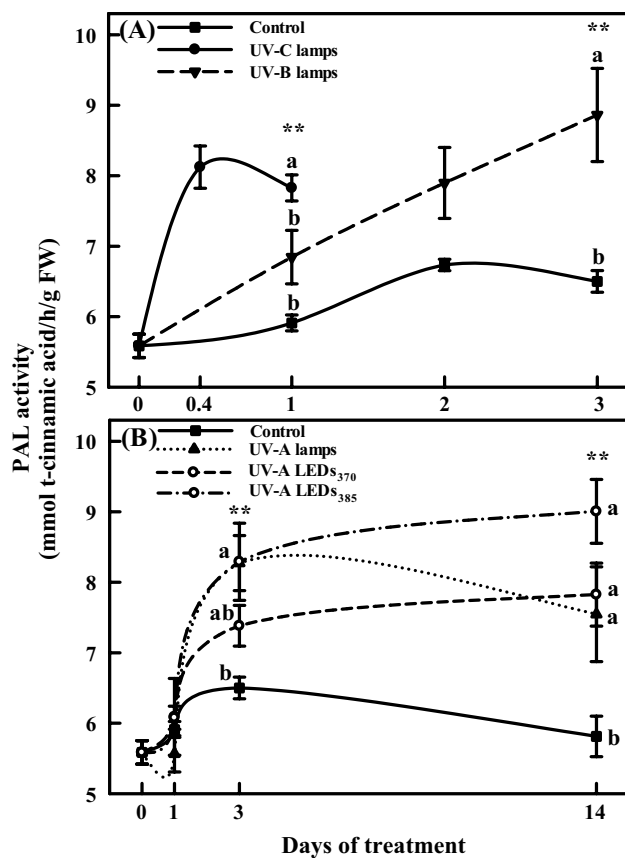


present study. However, this study confirmed that the shorter the UV wavelength, the faster the  $F_v/F_m$  value decreased, although the UV energy ( $W\ m^{-2}$ ) of all UV treatments was equally adjusted, unlike that in previous UV-related studies. Therefore, this result implies that characteristics of the UV wavelength have a greater effect on plant stress than does integrated UV energy.

## 4.2 Growth characteristics

In this study, plants suffered from severe physiological disorders induced by UV-C lamps on day 3 of treatment, and by UV-B lamps on day 4 of treatment; therefore, sample collection was discontinued. Symptoms of physiological disorders appeared in dropwort plants exposed continuously to UV-C and UV-B lamps after just 2 days of irradiation (Fig. 4a). Typically, most UV light reaching the leaf surface (approximately 80%) is reflected by the wax layer of the epidermal

cells. Further, plants alter the structure of the epicuticular wax layer, or induce the formation of additional waxes, to minimize the damage generated by UV irradiation (Mulroy 1979; Tevini and Steinmüller 1987; Lee et al. 2014). Thus, the glossy leaves observed in the present study were probably induced by wax layer formation (data not shown). Negative effects of UV irradiation on plant growth have been widely reported in previous studies. UV irradiation damages PS I and II; inhibits the activity of rubisco, which is a crucial enzyme for fixing  $CO_2$ ; destroys photosynthetic factors such as chlorophylls and carotenoids; and induces stomatal closure, thereby reducing the growth rate (Strid et al. 1990; Mackerness 2000; Hollósy 2002). In contrast, no physiological disorders or negative effects on dropwort growth were observed in plants treated with UV-A until day 14 of treatment (Fig. 4b). UV-A LED-treated plants had a similar growth rate to that of the control plants on day 14 of treatment. Recent studies of UV-A radiation have



**Fig. 5** Phenylalanine ammonia-lyase (PAL) activity of dropwort plants exposed to ultraviolet (UV)-C and UV-B lamps (a) and UV-A lamps and UV-A light-emitting diodes (LEDs, b). Vertical bars indicate standard errors. Statistically significant differences are indicated at  $**p < 0.01$  ( $n = 5$ )

reported positive rather than negative effects of UV-A on plant growth (Xu and Gao 2010; Štroch et al. 2015), which have two likely explanations. First, the UV-A spectrum has a wavelength range near to 400 nm, which is in the visible light spectrum, and is recognized by photoreceptors such as phototropins and cryptochromes in the same way as blue light. Secondly, UV-A energy can be absorbed by chlorophylls and carotenoids to be used in photosynthesis (Lichtenthaler 1987; Johnson and Day 2002; Turnbull et al. 2013). These phenomena could explain why the effect of treatment with 385-nm UV-A LEDs was more remarkable on the maintenance of growth than that of the 370-nm UV-A LEDs (Table 2).

### 4.3 Total phenolic, total flavonoid, and persicarin content

UV light is a stress factor for plants, which leads to the generation of ROS that damage DNA, RNA, proteins, chloroplasts, and photosynthetic pigments (Hideg et al. 2013;

Lee et al. 2017). However, plants are known to accumulate UV-absorbing compounds, such as phenolic compounds like flavonoids, as a defense mechanism against UV irradiation (Jenkins 2009). These UV-absorbing compounds accumulate in the epidermal cells to block the transmission of UV to mesophyll cells—the main site of photosynthesis—or to quench the ROS generated by UV irradiation (Stapleton 1992; Braun and Tevini 1993; Behn et al. 2011). Consistent with these results, in the present study we found that UV irradiation enhanced levels of phenolic compounds, although the effects were different depending on the UV wavelength. Irradiation with UV-C and UV-B lamps for 2 days had little positive effect on plants' total phenolic and flavonoid contents. This may be explained by the high-energy wavelengths causing continuous generation of ROS. In contrast, treatment of plants with UV-A increased their total phenolic and flavonoid contents on day 1 and 3 of treatment, and, compared to control plants, the total phenolic content did not decline until day 14 of treatment. UV-A wavelengths induced the accumulation of flavonols in *Mesembryanthemum crystallinum* leaves (Ibdah et al. 2002). Persicarin, a flavonoid that absorbs UV light, is the major substance that mediates the pharmacological effects of dropwort plants such as alcohol detoxification and hepatoprotection (Park and Choi 1997; Park et al. 2002), neuroprotection (Ma et al. 2010), anti-inflammation (Kim et al. 2013), and anti-obesity. Persicarin might be used as a target compound to determine the nutritional quality of dropwort plants because it is highly stable during beverage preparation processes, such as in the production of green vegetable juice. A clear effect of UV wavelength on persicarin content was observed throughout the irradiation period. Among all UV treatment conditions, UV-A enhanced the accumulation of persicarin more than did UV-B and UV-C treatments. Comparing the ecological stress caused by high and low exposure to UV-B, Hideg et al. (2013) reported that low doses of UV-B induced eustress (stress that creates positive results) by increasing the activity of genes involved in antioxidant defense. Meanwhile, Flint and Caldwell (2003) calculated the effective UV dose in biological aspect using the action spectrum depending on the wavelength. Thus, the present study suggests that the optimum dose of UV irradiation required to increase the content of bioactive compounds changes based on the UV wavelength, even though the energy level of UV irradiation remains the same.

### 4.4 Anthocyanin content

Compared to water dropwort, the red-colored small dropwort plant has higher marketability because of its higher availability as plant material for functional foods such as green vegetable juice. Leaves of dropwort plants grown under limited water conditions showed higher D3G and C3G

contents than controls (Lee and Oh 2017). Anthocyanins, which have strong antioxidant activity, are water-soluble flavonoid pigments (Kong et al. 2003), generally found in the plant vacuole or cytoplasm in the form of glycosides such as delphinidin 3-*O*-glucoside and C3G (Choung 2004). Anthocyanins are readily synthesized when plants are placed under stressful conditions by various environmental changes (Steyn et al. 2002; Makoi et al. 2010; Cisowska et al. 2011). In particular, UV stress effectively induces accumulation of anthocyanin in plants (Tsormpatsidis et al. 2008, 2010; Wang et al. 2012). Three anthocyanins, D3G, C3G, and P3G, were detected in dropwort plants exposed to UV irradiation. D3G constituted 42% of the total anthocyanin content, and C3G constituted 55%. All dropwort plants exposed to UV maintained a higher anthocyanin content than controls throughout the UV irradiation period. Despite the short irradiation time (2 days), UV-C and UV-B lamps led to a higher accumulation of anthocyanins than in controls. However, UV-C lamps seem to be inappropriate UV light sources for enhancing anthocyanin content because they have a detrimental physiological effect on the leaves. UV-A lamps with a broad wavelength, including the UV-B spectrum, are more effective for accumulation of anthocyanins than UV-C or UV-B lamps, but a longer exposure to UV-A lamps or LEDs is required than for UV-C or UV-B lamps.

#### 4.5 PAL activity

PAL, the gateway enzyme of the phenylpropanoid pathway, is not only activated by several environmental stresses, but also acts sensitively as an adaptation mechanism for fluctuating environmental conditions (Oh et al. 2009). In addition, activated chalcone synthase (CHS), related to the biosynthetic pathway of flavonoids by UV irradiation, induced the accumulation of phenolic compounds, flavonoids, and anthocyanins (Hahlbrock and Scheel 1989; Braun and Tevini 1993; Lee et al. 2013). In the present study, regardless of UV wavelength, the activity of PAL was significantly higher in plants exposed to UV treatments than in the control plants. However, the activity of PAL differed depending on the UV wavelength throughout the irradiation periods. Following treatment with UV-C lamps, PAL activity was quickly activated after 0.4 days of treatment, and was highest on day 1 of treatment. UV-B lamps, UV-A lamps, and 385-nm UV-A LEDs induced significantly higher PAL activity in plants than in controls after 3 days of treatment, and all UV-A treatments induced significantly higher activity than in controls after 14 days of treatment. This supports the results showing enhancement of bioactive compounds, including anthocyanins, under UV irradiation.

Plant responses to UV depend on the rate, duration, dose, and wavelength of the UV irradiation (Pontin et al. 2010). In the present study, irradiation with UV-C and UV-B lamps

induced physiological disorders in plants within a short period, even though the plants were irradiated at the same energy level ( $\text{W m}^{-2}$ ) as other UV-A treatments. Temporary irradiation of dropwort plants with UV-B and UV-A had a positive effect on the accumulation of bioactive compounds, but UV-C treatment had a negative effect. In particular, irradiation with UV-A LEDs effectively enhanced bioactive compounds without adverse effects on growth. Further studies using various UV-A LEDs are required to determine the effect of specific wavelengths on growth characteristics and the accumulation of bioactive compounds in plants.

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#### References

- Ainsworth EA, Gillespie KM (2007) Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin–Ciocalteu reagent. *Nat Protoc* 2:875–877
- An WB, Lee BY (1991) Basic studies on the development hydroponic system of water dropwort, *Oenanthe stolonifera* DC. *J Korean Soc Hortic Sci* 32:425–433
- Behn H, Schurr U, Ulbrich A, Noga G (2011) Development-dependent UV-B responses in red oak leaf lettuce (*Lactuca sativa* L.): physiological mechanisms and significance for hardening. *Eur J Hortic Sci* 76:33–40
- Boo HO, Heo BG, Gorinstein S, Chon SU (2011) Positive effects of temperature and growth conditions on enzymatic and antioxidant status in lettuce plants. *Plant Sci* 181:479–484
- Braun J, Tevini M (1993) Regulation of UV-protective pigment synthesis in the epidermal layer of rye seedlings (*Secale cereale* L. cv. Kustro). *Photochem Photobiol* 57:318–323
- Choung MG (2004) Analysis of anthocyanins. *Korean J Crop Sci* 49:55–67
- Choung MG (2008) Optimal HPLC condition for simultaneous determination of anthocyanins in black soybean seed coats. *Korean J Crop Sci* 53:359–368
- Cisowska A, Wojnicz D, Hendrich A (2011) Anthocyanins as antimicrobial agents of natural plant origin. *Nat Prod Commun* 6:149–156
- Dewanto V, Wu X, Adom KK, Liu RH (2002) Thermal processing enhances the nutritional value of tomatoes by increasing total antioxidant activity. *J Agric Food Chem* 50:3010–3014
- Flint SD, Caldwell MM (2003) A biological spectral weighting function for ozone depletion research with higher plants. *Physiol Plant* 117:137–144
- Frohnemeyer H, Staiger D (2003) Ultraviolet-B radiation-mediated responses in plants. Balancing damage and protection. *Plant Physiol* 133:1420–1428
- Fu W, Li P, Wu Y (2012) Effects of different light intensities on chlorophyll fluorescence characteristics and yield in lettuce. *Sci Hortic* 135:45–51
- Groom Q, Baker NR (1992) Analysis of light-induced depressions of photosynthesis in leaves of a wheat crop during the winter. *Plant Physiol* 100:1217–1223

- Hahlbrock H, Scheel D (1989) Physiology and molecular biology of phenylpropanoid metabolism. *Ann Rev Plant Mol Biol* 40:347–369
- Hideg É, Jansen MAK, Strid Å (2013) UV-B exposure, ROS, and stress: inseparable companions or loosely linked associates? *Trends Plant Sci* 18:107–115
- Hollósy F (2002) Effects of ultraviolet radiation on plant cells. *Micron* 33:179–197
- Hwang CR, Hwang IG, Kim HY, Kang TS, Kim YB, Joo SS, Lee JS, Jeong HS (2011) Antioxidant component and activity of dropwort (*Oenanthe javanica*) ethanol extracts. *Korean J Soc Food Sci Nutr* 40:316–320
- Hwang SJ, Park SJ, Kim JD (2013) Component analysis and antioxidant activity of *Oenanthe javanica* extracts. *J Korean Food Sci Technol* 45:227–234
- Ibdah M, Krins A, Seidlitz HK, Heller W, Strack D, Vogt T (2002) Spectral dependence of flavonol and betacyanin accumulation in *Mesembryanthemum crystallinum* under enhanced ultraviolet radiation. *Plant Cell Environ* 25:1145–1154
- Jenkins GI (2009) Signal transduction in responses to UV-B radiation. *Ann Rev Plant Biol* 60:407–431
- Johnson GA, Day TA (2002) Enhancement of photosynthesis in Sorghum bicolor by ultraviolet radiation. *Physiol Plant* 116:554–562
- Jordan BR, Chow WS, Strid Å, Anderson JM (1991) Reduction in cab and psbA RNA transcripts in response to supplementary ultraviolet-B radiation. *FEBS Lett* 284:5–8
- Jordan BR, James PE, Strid Å, Anthony RG (1994) The effect of ultraviolet-B radiation on gene expression and pigment composition in etiolated and green pea leaf tissue: UV-B induced changes are gene-specific and dependent upon the developmental stage. *Plant Cell Environ* 17:45–54
- Kim TH, Ku SK, Bae JS (2013) Persicarin is anti-inflammatory mediator against HMGB1-induced inflammatory responses in HUVECs and in CLP-induced sepsis mice. *J Cell Physiol* 228:696–703
- Kong JM, Chia LS, Goh NK, Chia TF, Brouillard R (2003) Analysis and biological activities of anthocyanins. *Phytochemistry* 64:923–933
- Lee JY, Oh MM (2017) Mild water deficit increases the contents of bioactive compounds in dropwort. *Hortic Environ Biotechnol* 58:458–466
- Lee HY, Yoo MJ, Chung HJ (2001) Antibacterial activities in watercress cultivated with different culture methods. *Korean J Food Cult* 16:243–249
- Lee KI, Rhee SH, Park KY (2004) Antimutagenic and antioxidative effects of water dropwort and small water dropwort. *Korean J Commu Living Sci* 15:49–55
- Lee MJ, Son JE, Oh MM (2013) Growth and phenolic content of sowthistle grown in a closed-type plant production system with a UV-A or UV-B lamp. *Hortic Environ Biotechnol* 54:492–500
- Lee MJ, Son JE, Oh MM (2014) Growth and phenolic compounds of *Lactuca sativa* L. grown in a closed-type plant production system with UV-A, -B, or -C lamp. *J Sci Food Agric* 94:197–204
- Lee HJ, Chun JH, Kim SJ (2017) Effects of pre harvest light treatments (LEDs, fluorescent lamp, UV-C) on glucosinolate contents in rocket salad (*Eruca sativa*). *Hortic Sci Technol* 35:178–187
- Lichtenthaler HK (1987) Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. *Methods Enzymol* 148:350–382
- Lidon FJC, Reboredo FH, Leitão AE, Silva MMA, Duarte MP, Ramalho JC (2012) Impact of UV-B radiation on photosynthesis—an overview. *Emir J Food Agric* 24:546–556
- Lydie HT, Laurent C, José LG, Philippe M, Soulaïman S, Nathalie L (2016) Light signaling and plant responses to blue and UV radiation—perspectives for applications in horticulture. *Environ Exp Bot* 121:22–38
- Ma CJ, Lee KY, Jeong EJ, Kim SH, Park J, Choi YH, Kim YC, Sung SH (2010) Persicarin from water dropwort (*Oenanthe javanica*) protects primary cultured rat cortical cells from glutamate-induced neurotoxicity. *Phytother Res* 24:913–918
- Mackerness SAH (2000) Plant responses to ultraviolet-B (UV-B: 280–320 nm) stress: what are the key regulators? *Plant Growth Regul* 32:27–39
- Mackerness SAH, John CF, Jordan B, Thomas B (2001) Early signaling components in ultraviolet-B responses: distinct roles for different reactive oxygen species and nitric oxide. *FEBS Lett* 489:237–242
- Makoi JH, Belane AK, Chimphango S, Dakora FD (2010) Seed flavonoids and anthocyanins as markers of enhanced plant defence in nodulated cowpea (*Vigna unguiculata* L. Walp.). *Field Crop Res* 118:21–27
- Maxwell K, Johnson GN (2000) Chlorophyll fluorescence—a practical guide. *J Exp Bot* 51:659–668
- Mulroy TW (1979) Spectral properties of heavily glaucous and non-glucous leaves of a succulent rosette-plant. *Oecologia* 38:349–357
- Nedunchezian N, Kulandaivelu G (1997) Changes induced by ultraviolet-B (280–320 nm) radiation to vegetative growth and photosynthetic characteristics in field grown *Vigna unguiculata* L. *Plant Sci* 123:85–92
- Oh MM, Trick HN, Rajashekar CB (2009) Secondary metabolism and antioxidants are involved in environmental adaptation and stress tolerance in lettuce. *J Plant Physiol* 166:180–191
- Park JC, Choi JW (1997) Effects of methanol extract of *Oenanthe javanica* on the hepatic alcohol-metabolizing enzyme system and its bioactive component. *Phytother Res* 11:260–262
- Park JC, Yu YB, Lee JH (1993) Isolation of steroids and flavonoids from the herb of *Oenanthe javanica* DC. *Korean J Pharmacogn* 24:244–246
- Park JC, Young HS, Yu YB, Lee JH (1995) Isorhamnetin sulphate from the leaves and stems of *Oenanthe javanica* in Korea. *Planta Med* 61:377–378
- Park JC, Hur JM, Park JG (2002) Biological activities of Umbelliferae family plants and their bioactive flavonoids. *Food Ind Nutr* 7:30–34
- Pitzschke A, Forzani C, Hirt H (2006) Reactive oxygen species signaling in plants. *Antioxid Redox Signal* 8:1757–1764
- Pontin MA, Piccoli PN, Francisco R, Bottini R, Martínez-Zapater JM, Lijavetzky D (2010) Transcriptome changes in grapevine (*Vitis vinifera* L.) cv. Malbec leaves induced by ultraviolet-B radiation. *BMC Plant Biol* 10:224–237
- Seo WH, Baek HH (2005) Identification of characteristic aroma-active compounds from water dropwort (*Oenanthe javanica* DC.). *J Agric Food Chem* 53:6766–6770
- Sicora C, Szilárd A, Sass L, Turcsányi E, Máté A, Vass I (2006) UV-B and UV-B radiation effects on photosynthesis at the molecular level. In: Ghetti F, Checcucci G, Bornman JF (eds) *Environmental UV radiation: impact on ecosystems and human health and predictive models*. Springer, Dordrecht, pp 121–135
- Singh S, Kumari R, Agrawal M, Agrawal SB (2011) Modification in growth, biomass and yield of radish under supplemental UV-B at different NPK levels. *Ecotoxicol Environ Saf* 74:897–903
- Son KH, Oh MM (2013) Leaf shape, growth and antioxidant phenolic compounds of two lettuce cultivars grown under various combinations of blue and red light-emitting diodes. *HortScience* 48:988–995
- Son MJ, Cha CG, Park JH, Kim CS, Lee SP (2005) Manufacture of dropwort extract using brown sugar, fructose syrup and oligosaccharides. *Korean J Soc Food Sci Nutr* 34:1485–1489
- Stapleton AE (1992) Ultraviolet radiation and plants: burning questions. *Plant Cell* 4:1353–1358
- Steyn W, Wand S, Holcroft D, Jacobs G (2002) Anthocyanins in vegetative tissues: a proposed unified function in photoprotection. *New Phytol* 155:349–361

- Strid Å, Chow WS, Anderson JM (1990) Effects of supplementary ultraviolet-B radiation on photosynthesis in *Pisum sativum*. *Biochim Biophys Acta* 1020:260–268
- Štroch M, Materová Z, Vrábl D, Karlický V, Šigut L, Nezval J, Špunda V (2015) Protective effect of UV-A radiation during acclimation of the photosynthetic apparatus to UV-B treatment. *Plant Physiol Biochem* 96:90–96
- Tevini M, Steinmüller D (1987) Influence of light. UV-B radiation, and herbicides on wax biosynthesis of cucumber seedlings. *Plant Physiol* 131:111–121
- Tsormpatsidis E, Henbest RGC, Davis FJ, Battey NH, Hadley P, Wagstaffe A (2008) UV irradiance as a major influence on growth, development and secondary products of commercial importance in Lollo Rosso lettuce Revolution grown under polyethylene films. *Environ Exp Bot* 63:232–239
- Tsormpatsidis E, Henbest RGC, Battey NH, Hadley P (2010) The influence of ultraviolet radiation on growth, photosynthesis and phenolic levels of green and red lettuce: potential for exploiting effects of ultraviolet radiation in a production system. *Ann Appl Biol* 156:357–366
- Turnbull TL, Barlow AM, Adams MA (2013) Photosynthetic benefits of ultraviolet-A to *Pimelea ligustrina*, a woody shrub of sub-alpine Australia. *Oecologia* 173:375–385
- Vass I, Szilárd A, Sicora C (2005) Adverse effects of UV-B light on the structure and function of the photosynthetic apparatus. In: Pessarakli M (ed) *Handbook of photosynthesis*, 2nd edn. CRC Press, Taylor & Francis Publishing Company, New York, pp 827–843
- Wang Y, Zhou B, Sun M, Li Y, Kawabata S (2012) UV-A light induces anthocyanin biosynthesis in a manner distinct from synergistic blue + UV-B light and UV-A/blue light responses in different parts of the hypocotyls in turnip seedlings. *Plant Cell Physiol* 53:1470–1480
- Wu X, Gu L, Prior RL, McKay S (2004) Characterization of anthocyanins and proanthocyanidins in some cultivars of *Ribes*, *Aronia* and *Sambucus*. *J Agric Food Chem* 52:7846–7856
- Xu J, Gao K (2010) UV-A enhanced growth and UV-B induced positive effects in the recovery of phytochemical yield in *Gracilaria lemaneiformis* (Rhodophyta). *J Photochem Photobiol B Biol* 100:117–122
- Yang JH, Kim SC, Shin BY, Jin SH, Jo MJ, Jegal KH, Kim YW, Lee JR et al (2013) O-methylated flavonol isorhamnetin prevents acute inflammation through blocking of NF-KB activation. *Food Chem Toxicol* 59:362–372