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End-of-production Ultraviolet A and Blue Light Similarly Increase Lettuce Coloration and Phytochemical Concentrations

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Abstract. **Anthocyanins are a group of human-health-promoting phenolic compounds that influence the pigmentation of red-leaf lettuce (*Lactuca sativa*). Ultraviolet A (UVA; 315–399 nm) and blue (B; 400–499 nm) light can increase the concentrations of phenolic compounds but also suppress cellular expansion, which can limit harvestable biomass accumulation. It is not known whether UVA or B light is more effective at increasing phenolic compound concentrations when they are each applied at the same photon flux density. Our objective was to evaluate the efficacy of UVA and B light when added during the end of production (EOP) at promoting phenolic compound synthesis and red-leaf coloration without limiting biomass accumulation. We grew red-leaf lettuce 'Rouxai' in a controlled indoor environment at an air temperature of 22 °C under warm-white and red light-emitting diodes (LEDs). On day 24, 30 or 60 μmol·m^{-2}·s^{-1} from UVA, B, UVA plus B, or red plus green LEDs was added during the last 6 days of the 30-day production period. UVA and B light, alone or combined, similarly increased leaf redness (by up to 72%), total phenolic concentration (by up to 92%), total anthocyanin concentration (by up to 2.7-fold), and relative chlorophyll concentration (by up to 20%) and did not inhibit growth, compared with lettuce grown without EOP supplemental lighting. Considering B light was as effective as UVA light at increasing leaf color and phytonutrient density and that B LEDs are more electrically effective, economical, and durable, an enriched blue-light spectrum at the EOP is a comparatively sustainable method to increase crop quality without suppressing biomass accumulation.**

Indoor vertical farming of leafy green vegetables continues to expand because of its efficient use of land, water, and fertilizer, and no use of pesticides (Kozai and Niu 2016). Furthermore, the ability to automate most or all cultivation practices and grow near or in large cities can decrease labor and transportation costs compared with field production. Although commercial growers control and optimize environmental factors in indoor farms, such as temperature, carbon dioxide (CO_2) concentration, water vapor pressure deficit, and light, they are entirely reliant on electricity. Therefore, in the absence of sunlight, electric lighting is one of the most expensive capital and operational expenses, and the least sustainable characteristic, of an indoor farm (Kozai and Niu 2016). Light-emitting diodes (LEDs) are commonplace in indoor farms because of their increasingly high efficacies and longer lifetimes (Kusuma et al. 2020), which have made LEDs more effective than conventional lighting fixtures, such as high-pressure sodium lamps (Radetsky 2018). Additionally, LEDs have the advantage of precisely controlling the light spectrum for specific plant applications.

Lettuce (*Lactuca sativa*) is a compact leafy green with a short production cycle, which in combination with its high consumer demand, makes it the most grown species in indoor farms. It is one of the most widely consumed vegetables in the United States (US Department of Agriculture 2018) because of its versatile culinary use and nutritional value (Kim et al. 2016). Lettuce is also a model crop in horticultural lighting research because of its responsiveness to the light spectrum and flux density. For instance, manipulating the light environment in controlled environments influences lettuce biomass accumulation, plant and leaf morphology, and concentrations of bioactive compounds (Kitazaki et al. 2018; Shin et al. 2014; Son et al. 2017; Vaštakaitė-Kairienė et al. 2021).

Supplementing the light spectrum with short-wavelength light, such as ultraviolet A (UVA; 315–399 nm) and blue (B; 400–499 nm), can affect plant traits such as extension growth, nutritional quality, and leaf coloration. At least a moderate intensity of B light typically suppresses extension growth, leading to a smaller leaf area than plants grown with little or no B light (Briggs and Huala 1999; Cosgrove 1981; Son and Oh 2013). For example, 23 μmol·m^{-2}·s^{-1} of B light was enough to suppress fresh weight compared with the 100% R light control, and higher intensities further suppressed growth (Son and Oh 2013). The smaller leaf area decreases the surface area and thus light interception, which can decrease biomass accumulation. For example, lettuce 'Rouxai' grown under 200 μmol·m^{-2}·s^{-1} of white light supplemented with 50 μmol·m^{-2}·s^{-1} of B (peak = 449 nm) had less shoot biomass than plants grown under other supplemental wavelengths, such as an additional 50 μmol·m^{-2}·s^{-1} of green (G; 500–599 nm; peak = 526 nm) light (Vaštakaitė-Kairienė et al. 2021) Additionally, as the percentage of B light in a red (R; 600–699 nm) + B spectrum increased, lettuce shoot fresh mass was less than that grown under a light spectrum with a higher R:B (Lee et al. 2010; Son and Oh 2013). To date, few studies have compared UVA and B light on mediating plant growth. In one study, lettuce 'Red Butter' and 'Yanzhi' grown under 250 μmol·m^{-2}·s^{-1} of white light supplemented with 10 μmol·m^{-2}·s^{-1} of UVA (peak = 380 nm) light had lower shoot fresh and dry mass than those grown without supplemental light or other wavelengths, such as far-red or far-red+UVA light (He et al. 2021). In another study, supplemental UVA light slightly increased lettuce 'Hongyeom' fresh mass (Lee et al. 2013), indicating that the effects of UVA light on lettuce growth are inconsistent and likely cultivar dependent.

Fresh mass accumulation directly affects yield and profitability, but quality attributes such as nutritional density, leaf coloration, and taste are also important traits for growers, as well as consumers, and may affect the latter's willingness to buy a product. UVA and B light can potentially increase nutritional quality by increasing the concentration of various secondary metabolites and vitamins (Alrifai et al. 2019; Hasan et al. 2017; Thoma et al. 2020). Phenolic compounds are one of the most abundant secondary metabolites in plants; they help protect against abiotic and biotic stresses, are involved in pigment accumulation, and influence taste (Balasundram et al. 2006; Naikoo et al. 2019; Soares et al. 2013). Phenolic compounds are antioxidants that have numerous potential health benefits to humans, such as antiallergenic, anti-inflammatory, cardioprotective, and vasodilatory properties (Balasundram et al. 2006). These bioactive phenolic compounds are not synthesized in mammalian tissues, which makes their

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acquisition in the diet from plant sources such as fruits and vegetables essential (Lin et al. 2016). Lettuce phenolic concentrations can increase under small doses of UVA light. For example, in lettuce 'Hongyeom', total phenolic concentration (TPC) increased by 30% when 11 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of UVA (peak = 352 nm) light was added to 185 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of white light (Lee et al. 2013). Conversely, an increase in the photon flux density (PFD) of UVA (peak = 373 nm) from 5 to 21 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in a white-light background did not affect TPC (Li and Kubota 2009). B light has a more consistent effect on lettuce TPC. For instance, lettuce 'Sunmang' and 'Grand Rapids TBR' TPC increased by up to 200% when the percentage of B light in an R+B spectrum increased from 0% to 59% (Son and Oh 2013). Additionally, lettuce 'Rouxai' TPC increased by ~25% relative to the control when 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light was added to the light spectrum (Vaštakaitė-Kairienė et al. 2021). Therefore, although UVA and B light both have the potential to increase TPC in lettuce and B light may be more effective, more research is needed because no studies have compared their efficacy at the same PFD and duration.

Anthocyanins are a subset of plant phenolic compounds that play a significant role in influencing red-leaf pigmentation, especially in red- and purple-leaf plants such as red-leaf lettuce. In general, a light spectrum that increases the TPC in lettuce also increases total anthocyanin concentration (TAC). For example, TAC in lettuce 'Red Cross' increased by 11% when the PFD of UVA increased (Li and Kubota 2009). In the same study, lettuce TAC increased by 30% as the B light percentage increased from 23% to 55% in a white-light background. Finally, lettuce 'Hongha' TAC increased by up to 6.9-fold as the percentage of B light in an R+B spectrum increased to 43% (Lee et al. 2010).

End-of-production (EOP) lighting refers to adding additional light to a light spectrum for a short period (e.g., several days) before the harvest or modifying the PFD. EOP white-red light of different PFDs (0–470 $\mu mol \cdot m^{-2} \cdot s^{-1}$) was added to the last 6 or 7 d of production and increased lettuce nutritional quality and improved postharvest performance indicators such as appearance, texture, and odor (Min et al. 2021). EOP lighting can be a potentially useful technique to mitigate possible disadvantages of using a high PFD of UVA or B light throughout production, such as less fresh mass accumulation, while enhancing the nutritional quality and red-leaf pigmentation. EOP lighting can lower electrical costs by only delivering an enriched spectrum for a limited portion of the production cycle compared with the entire time. Therefore, we grew lettuce 'Rouxai' under various EOP treatments to 1) determine how EOP lighting with UVA and B light influences biomass accumulation, TPC, TAC, and leaf coloration and 2) to compare the effects of UVA and B light when applied at the same PFD. We hypothesized that 1) both UVA and B light would slightly inhibit plant growth and 2) UVA and B light would be equally effective at increasing TPC, TAC, and leaf coloration when delivered at the same PFD.

Materials and Methods

Plant material and propagation conditions. The red-leaf lettuce cultivar 'Rouxai' (Johnny's Selected Seeds, Winslow, ME, USA) was selected for this study because of its commercial relevance, sensitivity to the light spectrum, and relevant previous experiments. On 21 May 2019 Replication (Rep.) 1 and 23 Jun 2019 (Rep. 2), we presoaked 200-cell (2.5 cm × 2.5 cm) rockwool plugs (AO 25/40 Starter Plugs; Grodan, Milton, ON, Canada) in deionized water with a pH of 4.5 and sowed 200 seeds of lettuce 'Rouxai' that were presoaked in deionized water with a pH of 4.5. The pH was adjusted using 10% sulfuric acid (H_2SO_4). H_2SO_4 and all other chemicals used during this experiment were purchased from Sigma-Aldrich (Merck KGaA, Darmstadt, Germany). From seed sow to day 7, clear plastic humidity domes covered the trays. We grew the lettuce seedlings in a temperature-controlled growth room (the Controlled Environment Lighting Laboratory at Michigan State University) at 23 °C throughout each replication. We germinated the seeds under a total PFD (TPFD; 315–800 nm) of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ delivered from warm-white (WW; peak = 639 nm, correlated color temperature = 2700 K) LEDs (PHYTOFY RL; OSRAM, Beverley, MA, USA) controlled by customized software (Spartan Control Software; OSRAM) for 24 $h \cdot d^{-1}$. Beginning on day 3, seedlings were grown under a TPFD of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from R (peak = 664 nm) plus 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from WW LEDs for 20 $h \cdot d^{-1}$ (daily light integral = 12.96 $mol \cdot m^{-2} \cdot d^{-1}$) until EOP treatments began. We hand-watered the seedlings until transplant on day 10 with deionized water supplemented with a water-soluble fertilizer ($12N–4P_2O_5–16K_2O$ RO Hydro FeED; JR Peters, Inc., Allentown, PA, USA) and magnesium sulfate (Epsom salt; Pennington Seed, Inc., Madison, GA, USA) to achieve the following nutrient solution (in $mg \cdot L^{-1}$): 125 N, 42 P, 167 K, 73 Ca, 49 Mg, 39 S, 1.7 Fe, 0.52 Mn, 0.56 Zn, 0.13 B, 0.47 Cu, and 0.13 Mo. The pH was 5.6 and the electrical conductivity (EC) was 1.6 $mS \cdot m^{-1}$, as measured by a pH/EC meter (HI9814; Hanna Instruments, Woonsocket, RI, USA).

Growth conditions and lighting treatments. We used two vertical hydroponic growing racks with three canopies each to create six EOP lighting treatments. On day 10, seedlings were transplanted into floating 36-cell rafts (Beaver Plastics, Ltd., Acheson, AB, Canada) with 2.5-cm-wide holes that were spaced 20 × 15 cm apart. The nutrient solution used in the hydroponic growing racks was the same mixture provided to the seedlings, but the concentrations were increased by 20% (e.g., 150 mg $N \cdot L^{-1}$). The pH and EC of the hydroponic tanks were measured (as previously described) daily and had an average of 5.8 and 1.7 $mS \cdot m^{-1}$, respectively. The pH was adjusted to 5.5 to 5.8 using potassium bicarbonate and H_2SO_4. The air temperature setpoint was 23 °C, although the actual air temperature was 23.5 ± 0.8 °C for each replication. Infrared sensors were used to monitor plant canopy temperature, which averaged 24.1 ± 0.8 °C (Rep. 1) and 24.7 ± 0.8 °C (Rep. 2). Relative humidity and CO_2 concentrations were not controlled but were measured at 51 ± 8% (Rep. 1 and 2) and 381 ± 18 ppm (Rep. 1) and 393 ± 19 ppm (Rep. 2), respectively. Additional information about the experimental conditions, equipment, and sensors can be found in Kelly et al. (2020).

On day 24, we added EOP supplemental lighting treatments to the original R+WW LED spectrum for the last 6 d of production using the same lighting fixtures previously described. EOP lighting treatments (Fig. 1; Table 1) consisted of a control (no additional light) or supplemental lighting from UVA (peak = 386 nm), B (peak = 449 nm), or G (peak = 532 nm) plus R LEDs. The EOP $G_{20}+R_{40}$ treatment was provided to evaluate EOP light with a higher TPFD but without additional UVA or B light. Treatments delivered a TPFD of 180 to 240 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 20 $h \cdot d^{-1}$. The TPFD and light spectrum of all lighting treatments were measured using a portable spectroradiometer (PS200; Apogee Instruments, Inc., Logan, UT, USA). Measurements were taken from nine representative spots at plant canopy level and averaged before the experiment began.

Biochemical analysis. Within each lighting treatment, we harvested three biological samples (leaf tissue from separate plants) for TPC analysis and TAC analysis. From each biological sample, we performed two or three technical replicates, depending on the assay. On day 30 after seed sow, we collected leaf tissue directly exposed to the lighting treatments from three randomly selected plants for TPC and TAC analysis, which we then froze in liquid nitrogen and stored in a −80 °C freezer until analysis. We determined lettuce 'Rouxai' TPC spectrophotometrically based on the Ainsworth and Gillespie (2007) protocol, with slight modifications. We mixed 0.5 g of frozen plant tissue from each biological sample with 5 mL of 80% methanol (≥99.9%) in a ceramic mortar. We then transferred the mixture to a 15 mL polypropylene conical centrifuge tube (Falcon; Fisher Scientific, Hampton, NH, USA) and incubated it for 24 h in a 4 °C refrigerator. Afterward, we centrifuged (Heraeus Megafuge; Thermo Fisher Scientific, Waltham, MA, USA) the samples for 5 min at a relative centrifugal force of 4000 g_n before filtering the supernatant through a 70-mm qualitative filter paper (Whatman Grade No. 1; Maidstone, United Kingdom) into a 2-mL Eppendorf microcentrifuge tube (Dot Scientific, Burton, MI, USA) that was stored in a –20 °C freezer. Next, we created three technical replicates by adding 100 µL of the filtrate to three different 1.5-mL plastic cuvettes (DOT Scientific). We diluted the filtrate with 200 µL of 10% (vol/vol) Folin and Ciocalteu's phenol reagent and 800

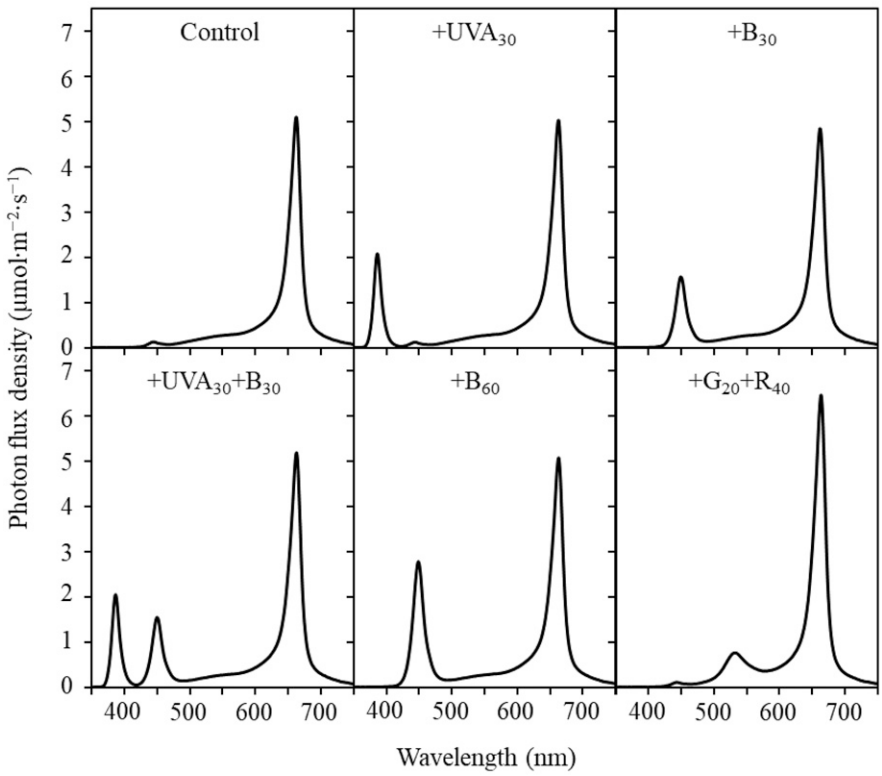

Fig. 1. The spectral distribution of the base warm-white and red light-emitting diode (LED) lighting spectrum plus end-of-production lighting treatments that were added for the last 6 d of production. End-of-production lighting treatments consisted of additional ultraviolet A (UVA; 315–399 nm) and/or blue (B; 400–499 nm) light or green (G; 500–599 nm) plus red (R; 600–699 nm) light.

μL of sodium carbonate (Na_2CO_3; ≥99.0%) and mixed cuvettes thoroughly before covering and leaving them to sit for 20 min at room temperature. We measured the absorbance of each biological and technical replicate at 765 nm using a spectrophotometer (BioSpec–mini; Shimadzu, Japan). We calculated the TPC in lettuce 'Rouxai' on a fresh weight ($mg \cdot g^{-1}$ FW) basis using a gallic acid (anhydrous) standard curve ($R^2 > 0.95$).

We determined the TAC of lettuce 'Rouxai' using a modified pH differential method (AOAC Official Method 2005.2) (Lee et al. 2005). We mixed 0.3 g of frozen plant tissue with 5 mL of 1% hydrochloric acid (ACS, ≥37.0%) in a ceramic mortar. Similar to the previous TPC protocol, we transferred the mixture to a 15-mL centrifuge tube and incubated it for 24 h in a 4 °C refrigerator. We centrifuged the samples for 5 min at a relative centrifugal force of 4000 g_n. We then filtered the supernatant through a 70-mm qualitative filter paper into a 2-mL Eppendorf tube and stored the supernatant in a –20 °C freezer. Next, we created two separate technical replicates, added 400 μL of the filtrate to two cuvettes, and mixed it with 2 mL of 0.025 M potassium chloride (KCL; ACS, ≥99.0%). Additionally, we added 400 μL of the filtrate to two other cuvettes and mixed it with 2 mL of 0.4 M sodium acetate (CH_3COONa; ACS, ≥99.0%). We covered all cuvettes, and after sitting for 20 min at room temperature, we measured the absorbance of each cuvette at 530 nm and 700 nm using the same spectrophotometer. The dilution factor was 6, and we calculated the TAC in each lettuce 'Rouxai' plant on a fresh weight ($mg \cdot g^{-1}$ FW) basis.

Morphological data collection and analysis. On day 30, we collected morphological data from 10 randomly selected plants that were not used for biochemical analysis from each treatment. We cut lettuce shoots at the substrate surface and weighed each one using an analytical balance (AG245; Mettler Toledo, Columbus, OH, USA). We dried the same shoots for 5 d at 60 °C in a drying oven (Blue M, Blue Island, IL, USA) then weighed each with the same balance. We measured leaf length and width (both in centimeters) of the fifth fully expanded leaf and counted leaf number (>2 cm in length). Additionally, we took overhead pictures of three randomly selected plants for reference and coloration analysis. We used the pictures to measure the $L^*a^*b^*$ color space of each photo using an R code developed to determine the lightness (black: $L^* = 0$; white: $L^* = 100$), redness (green: $a^* = -128$; red: $a^* = 127$), and blueness (blue: $b^* = -128$; yellow: $b^* = 127$) of each pixel in an imported TIFF picture. Finally, we measured the relative chlorophyll concentrations of each plant using a SPAD meter (SPAD-502; Konica Minolta Sensing, Inc., Osaka, Japan) by selecting 10 random plants from each treatment and measuring and averaging three spots on one fully expanded leaf directly exposed to light.

We arranged the experiment as a randomized complete block design with two replications in time (21 May 2019–20 Jun 2019; 23 Jun 2019–23 Jul 2019) and performed statistical analysis using R statistical analysis software (R Core Team 2014) (version 3.5.1; R Foundation for Statistical Computing, Vienna, Austria). We conducted analysis of variance and Tukey's honestly significant difference test ($\alpha = 0.5$) using the R packages 'dplyr' (Wickham et al. 2022) and 'agricolae' (Mendiburu 2021).

Table 1. End-of-production supplemental lighting treatments were provided to lettuce plants beginning on day 24. Except for the control, each treatment consisted of additional ultraviolet A (UVA; 315–399 nm) and/or blue (B; 400–499 nm) light or green (G; 500–599 nm) plus red (R; 600–699 nm) light, which increased the total photon flux density (TPFD; 315–800 nm) to 210 or 240 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and the extended daily light integral (eDLI, 315–800 nm) to 15.1 to 17.3 $mol \cdot m^{-2} \cdot d^{-1}$.

	Supplemental lighting ($\mu mol \cdot m^{-2} \cdot s^{-1}$)					
Treatment	UVA	Blue	Green	Red	TPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	eDLI ($mol \cdot m^{-2} \cdot d^{-1}$)
Control	0	0	0	0	180	13.0
UVA_{30}	30	0	0	0	210	15.1
B_{30}	0	30	0	0	210	15.1
$UVA_{30}+B_{30}$	30	30	0	0	240	17.3
B_{60}	0	60	0	0	240	17.3
$G_{20}+R_{40}$	0	0	20	40	240	17.3

Results

Total phenolic and anthocyanin concentration. The TPC of lettuce 'Rouxai' increased when we added UVA or B light to 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of WW+R light for the last 6 d of production (Fig. 2). However, there were no significant differences in the effectiveness of UVA or B light at increasing TPC. For instance, 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B (B_{30}) or UVA (UVA_{30}) light at the end of production increased TPC by 92% or 79%, respectively, compared with the control. Adding 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light to these treatments (B_{60}, $UVA_{30}+B_{30}$) did not further increase the TPC in 'Rouxai'. Increasing the TPFD without adding UVA or B light ($G_{20}+R_{40}$) provided an intermediate response and TPC was statistically similar to all of the other treatments.

Similar to TPC, TAC of lettuce 'Rouxai' increased when we added UVA or B light at the end of production (Fig. 2). UVA_{30}, B_{30}, $UVA_{30}+B_{30}$, or B_{60} for the last 6 d of production increased TAC by 224%, 258%, 303%, and 273%, respectively, compared

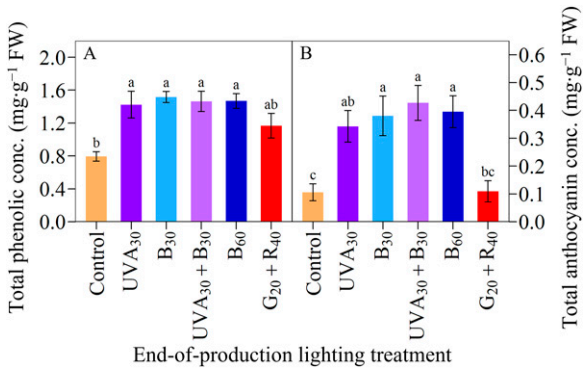

Fig. 2. (**A**) Mean total phenolic concentration and (**B**) total anthocyanin concentration on a fresh weight (FW) basis of lettuce 'Rouxai' grown without (control) or with supplemental end-of-production lighting of ultraviolet A (UVA; 315–399 nm), blue (B; 400–499 nm), green (G; 500–599 nm), and/or red (R; 600–699 nm) light for the last 6 d of production. The subscript value following each waveband represents its photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Each bar represents the mean of two replications with three biological samples per treatment and replication. Means with different letters are significantly different based on Tukey's honestly significant difference test ($\alpha = 0.05$). Error bars indicate the standard error of each treatment.

with the control. There were no significant differences in the effectiveness between the UVA_{30} and B_{30} treatments or the $UVA_{30}+B_{30}$ and B_{60} treatments. Likewise, the higher TPFD treatments containing UVA or B light did not increase TAC more than the lower TPFD treatments. Finally, $G_{20}+R_{40}$ did not increase TAC and was similar to the control and the UVA_{30} treatment.

Leaf pigmentation and relative chlorophyll concentration. $UVA_{30}+B_{30}$ or B_{60} added at the EOP increased 'Rouxai' leaf redness (more positive a* value) by 72% and 66%, respectively, compared with the control (Fig. 3). Increasing the TPFD without UVA or B light ($G_{20}+R_{40}$) did not increase leaf redness. Leaf redness under a lower TPFD of UVA or B light was similar to all other treatments. We also measured L* (darkness – lightness) and b* (blue – yellow) but there were no significant differences between any of the EOP treatments and the control (Fig. 3).

EOP lighting treatments containing UVA or B light increased the SPAD index (relative chlorophyll concentration) of lettuce 'Rouxai' (Fig. 3). For example, when we added UVA_{30} or B_{30} to the base WW+R spectrum, the SPAD index increased by 15% and 20%, respectively. The TPFD of UVA or B light did not differentially affect the SPAD index. The $G_{20}+R_{40}$ EOP lighting treatment did not affect the SPAD index.

Plant morphology and shoot mass. Plant morphology was generally similar under all EOP lighting treatments. No EOP treatment containing UVA or B light influenced leaf length, leaf width, or leaf number, except for B_{60}, which increased leaf number by 13% compared with the control. The $G_{20}+R_{40}$ treatment increased leaf width by 7% compared with the B_{60} treatment (Table 2). In addition, the EOP lighting treatments did not affect shoot fresh mass (Fig. 4), but some treatments slightly increased shoot dry mass (Table 2). Specifically, all EOP treatments that increased the TPFD by 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (B_{60}, $UVA_{30}+B_{30}$, $G_{20}+R_{40}$) increased shoot dry mass compared with the control treatment, irrespective of the light spectrum. For instance, the addition of $UVA_{30}+B_{30}$, B_{60}, or $G_{20}+R_{40}$ increased shoot dry mass by 35%, 32%, and 27%, respectively, but there was no statistical difference among those treatments.

Discussion

UVA and B light both increased secondary metabolite production and leaf pigmentation. Red-leaf lettuce has high concentrations of phenolic compounds, including anthocyanins, which influence its nutritional quality and taste. Environmental factors, including short-wavelength light, can differentially regulate the concentration of these metabolites, but there are inconsistent trends on what wavelengths and PFDs are most effective. Li and Kubota (2009) reported that partial substitution of white light with ~130 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B (peak = 476 nm) or 18 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of UVA (peak = 373 nm) light increased lettuce 'Red Cross' TAC by 31% and 11%, respectively, but neither affected TPC. In the current study, adding UVA_{30} or B_{30} to a WW+R light spectrum for the last 6 d of production increased the TPC and TAC of lettuce 'Rouxai' (Fig. 2). Interestingly, there were no differences in the effectiveness of UVA and B light, which contrasts with some other studies. For instance, when 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light (peak = 449 nm) was added to WW light for 18 d, TPC and TAC of baby leaf lettuce 'Rouxai' increased by 25% and 95%, respectively, but UVA (peak = 385 nm) at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ did not affect either TPC or TAC (Vaštakaitė-Kairienė et al. 2021). Discrepancies between these studies could be attributed to a variety of factors such as cultivar selection, plant maturity, UVA or B light application duration, PFD of UVA or B light applied, or the spectral quality and PFD of the background spectrum.

UVA and B light differentially regulate specific groups of phenolic compounds that lead to a cumulative increase in total content (Verdaguer et al. 2017). The largest group of phenolic compounds is flavonoids, from which anthocyanins are derived. Their strong absorption of ultraviolet and B light is often associated with an increased expression of genes that regulate flavonoid biosynthesis, such as those from the R2R3-MYB, WD40, and bHLH transcription factor families (Falcone Ferreyra et al. 2012; Naikoo et al.

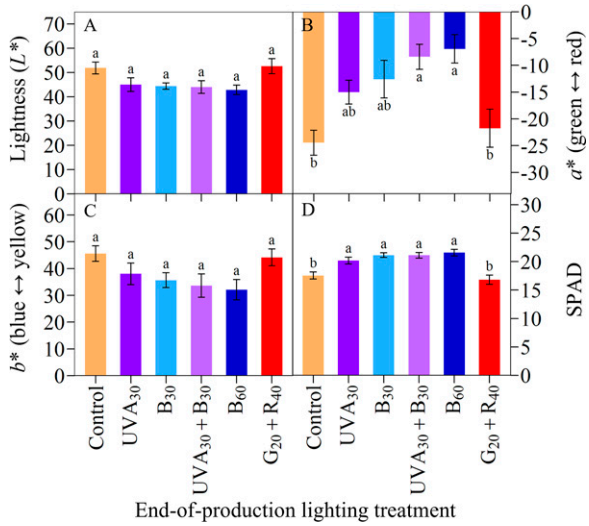

Fig. 3. (**A–C**) Mean leaf pigmentation indicated by L*a*b* values and (**D**) relative chlorophyll concentration (SPAD) of lettuce 'Rouxai' grown without (control) or with supplemental end-of-production lighting of ultraviolet A (UVA; 315–399 nm), blue (B; 400–499 nm), green (G; 500–599 nm), and/or red (R; 600–699 nm) light for the last 6 d of production. The subscript value following each waveband represents its photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Each bar represents the mean of two replications with three biological samples per treatment and replication, except for SPAD where there were 10 samples per treatment and replication. Means with different letters are significantly different based on Tukey's honestly significant difference test ($\alpha = 0.05$). Error bars indicate the standard error of each treatment.

Table 2. Shoot dry mass, leaf length, leaf width, and leaf number of lettuce 'Rouxai' grown without (control) or with supplemental end-of-production lighting of ultraviolet A (UVA; 315–399 nm), blue (B; 400–499 nm), green (G; 500–599 nm), and/or red (R; 600–699 nm) light for the last 6 d of production. The subscript value following each waveband represents its photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data are the mean of two replications with 10 samples in each replication. Means with different letters are significantly different according to Tukey's honestly significant difference test ($\alpha = 0.05$).

Treatment	Dry mass (g)	Leaf length (cm)	Leaf width (cm)	Leaf number
Control	1.59 b	12.8 a	20.1 ab	17.1 b
UVA_{30}	1.98 ab	13.0 a	19.7 ab	18.2 ab
B_{30}	1.88 ab	12.6 a	19.7 ab	18.4 ab
$UVA_{30}+B_{30}$	2.15 a	12.7 a	19.3 ab	18.3 ab
B_{60}	2.10 a	12.4 a	18.9 b	19.4 a
$G_{20}+R_{40}$	2.02 a	12.8 a	20.3 a	18.0 ab

2019; Zoratti et al. 2014). Cryptochromes, specifically cryptochrome 1 (cry1) and cryptochrome 2 (cry2), are the primary ultraviolet/B sensing photoreceptors and control many UV- and B-light responses (Briggs and Huala 1999). The increase in TPC and TAC in lettuce 'Rouxai' can be attributed to cry1's role in mediating flavonoid and anthocyanin biosynthesis by regulating the transcription of chalcone synthase (*CHS*), which encodes the first, committed enzyme in the flavonoid biosynthesis pathway (Jenkins et al. 2001; Wade et al. 2001; Weisshaar and Jenkinst 1998). Additionally, cry2 is involved in anthocyanin regulation, but only under low-intensity UV or B light because cry2 begins to degradeunder a higher PFD of these wavebands (Ahmad et al. 1998; Christie and Briggs 2001; Lin et al. 1998). This could explain why TPC or TAC did not increase in the present study when the PFD of UVA and/or B light at the end of production increased from 30 to 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$. We speculate that 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of short-wavelength light was sufficiently high to cause cry2 degradation and flavonoid synthesis to slow. It is also plausible that the cry1-mediated response was saturated with 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of UVA or B light.

In lettuce, red-leaf pigmentation is closely associated with anthocyanin accumulation in leaf tissue (Park et al. 2008), which suggests leaf coloration can be used as a predictor of anthocyanin content (Yang et al. 2016). Gazula and colleagues (2007) reported that anthocyanin concentrations in nine lettuce cultivars were closely associated with both instrument assessment of color and panelist rating of red coloration. Although there is a strong association between anthocyanin concentrations and red-leaf coloration in lettuce leaves, few studies have measured the effects of the light spectrum on both the anthocyanin concentration and coloration values of lettuce. Owen and Lopez (2015) quantified leaf coloration of multiple lettuce varieties grown in a greenhouse with or without various supplemental EOP lighting treatments. Leaf redness, and presumably anthocyanin concentration, increased after 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R, B, or R+B EOP lighting was applied for at least 3 d. In our study, the highest PFD tested (60 $\mu mol \cdot m^{-2} \cdot s^{-1}$) of UVA+B or B increased leaf redness compared with the control treatment (Fig. 3), which correlated with an increase in TAC.

UVA and blue light at the EOP did not suppress biomass accumulation. A moderate to high PFD of B light typically suppresses plant growth and leaf expansion (Cosgrove 1981; Ohashi-Kaneko et al. 2007; Shin et al. 2014; Son and Oh 2015), but the effects of UVA on plant growth are less clear and vary among species (Verdaguer et al. 2017). Some studies indicate that UVA can promote plant growth and leaf expansion (Chen et al. 2019; Hooks et al. 2021), whereas others report inhibitory effects, similar to B light (Krizek et al. 1998; Tsormpatsidis et al. 2008). In the present study, EOP lighting treatments did not increase shoot fresh mass (Fig. 4), but treatments with a TPFD of 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$, regardless of the spectrum, increased shoot dry mass by up to 35% compared with the control treatment. Because this biomass response was not specific to a light spectrum, the increase in shoot dry mass can be attributed to an increase in the daily light integral during the 6 d of EOP lighting (Kelly et al. 2020). The light spectrum before the EOP lighting treatments began was the same, so leaf area and therefore light interception can be assumed to be equal. Lettuce grown under EOP treatments with a TPFD of 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ had a greater shoot dry mass, but there were no morphological changes, except for B_{60}, which slightly inhibited leaf width compared with the $G_{20}+R_{40}$ treatment and had more leaves than the control treatment (Table 2).

UVA and B LEDs: technical considerations. While light from UVA and B LEDs can have similar effects on plant growth, morphology, and quality attributes at the end of lettuce production, there are differences in the LED types that need to be considered, such as photon efficacy ($\mu mol \cdot J^{-1}$), photon flux, and worker safety. From a horticultural perspective, the efficacy of an LED is the photon flux ($\mu mol \cdot s^{-1}$) per watt ($J \cdot s^{-1}$) of input power and thus represents an important performance metric (Kusuma et al. 2020). As of 2022, B LEDs have a photon efficacy of 1.6 to 3.5 $\mu mol \cdot J^{-1}$, whereas UVA LEDs have a photon efficacy of up to 0.9 $\mu mol \cdot J^{-1}$, but these values depend on peak wavelength, current density, and junction temperature (Kusuma et al. 2020, 2022). Because UVA LEDs produce fewer photons per unit of input power, more energy is required to deliver the same photon flux as B LEDs and thus, are less sustainable.

Another consideration is the effect of UVA and B light on worker safety and photopic vision. UVA photons are less energetic and thus less damaging to humans than ultraviolet B (280–315 nm) and UVC (100–280 nm) photons, but acute exposure can cause visual irritation, and long-term exposure can cause eye and skin damage (Burke and Wei 2009; Ivanov et al. 2018). B light is not as physiologically harmful to humans but can still cause visual irritation or photochemical damage with excessive exposure (Ouyang et al. 2020). Another concern of B light is the impact on the color rendering index (CRI) and correlated color temperature (CCT; K) of the work environment. The CRI is a scale of 0 to 100 that

Treatment	Control	UVA_{30}	B_{30}	$UVA_{30}+B_{30}$	B_{60}	$G_{20}+R_{40}$
Fresh mass (g)	70.0	73.7	73.8	72.9	74.7	73.8

Fig. 4. Shoot fresh mass (grams) of lettuce 'Rouxai' grown without (control) or with supplemental end-of-production lighting of ultraviolet A (UVA; 315–399 nm), blue (B; 400–499 nm), green (G; 500–599 nm), and/or red (R; 600–699 nm) light for the last 6 d of production. The subscript value following each waveband represents its photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data are the mean of two replications with 10 samples in each replication. There were no significant differences according to Tukey's honestly significant difference test ($\alpha = 0.05$). Pictures are representative plants from each treatment.

describes how well a light source reveals the true colors of objects. At a CRI of 0, all colors look the same and at a CRI of 100, all true colors of objects are apparent. CCT is the color temperature of a white-light source. The higher the CCT, the cooler (i.e., more blue and less red) the white light appears. Increasing the percentage of B in a light spectrum increases the CCT and generally lowers the CRI of a light source. Therefore, light with a low CRI (e.g., <80) can create a less desirable work environment for employees, cause visual eye strain, and make it more challenging to identify insects, diseases, or nutritional disorders. Because UVA light is less visible than B light, it has a negligible effect on the CRI and CCT of a light source.

EOP lighting as a production tool. Other studies have investigated the effects of EOP LED lighting on leafy greens production and have found it to be an effective method to increase plant growth and quality. For instance, lettuce 'Cherokee' grown in a greenhouse had increased leaf redness when 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of EOP R, B or R+B light was added for at least the last 3 d of production (up to 14 d) (Owen and Lopez 2015). Furthermore, 171 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of supplemental lighting that included low-wavelength B (peak = 403 nm) or R+B light in a greenhouse increased shoot fresh and dry mass, leaf area, TPC, TAC, and carotenoid concentration of lettuce 'Red Mist', but the magnitude depended on the daily light integral, duration of lighting (2 or 4 d), and whether it was applied at night or during the day (Hooks et al. 2021). In another study, anthocyanin content, but not phenolic content, of lettuce 'Codex' and 'Rouxai' increased 2-fold when high-intensity EOP light with a high percentage of B light (69% B + 31% R) was applied for the last 4 d of production (Gómez and Jiménez 2020). In the same study, EOP light with UVA light (5% UVA + 33% B + 62% R) did not increase anthocyanin or phenolic content. Finally, shoot fresh and dry mass, leaf area, leaf number, and TAC increased when 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of UVA (peak = 365 nm) light was applied to indoor-grown lettuce 'Klee' for 5 to 15 d before harvest (Chen et al. 2019). Similar to our results, EOP lighting with UVA increased TAC and shoot dry mass, although we applied a higher PFD and longer peak wavelength of UVA light. Therefore, EOP short-wavelength lighting can have little or no negative impact on leaf expansion or biomass accumulation, which can occur if delivered during the entire production period yet increase the nutritional quality and leaf coloration.

Conclusion

EOP lighting with short-wavelength light, such as UVA or B light, is a production technique that can enhance lettuce nutritional attributes, leaf coloration, and potentially biomass accumulation. Compared with continuous application of UVA or B light, EOP lighting with 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of UVA or B light had less of an effect on growth and leaf expansion inhibition but increased phenolic and anthocyanin concentrations as well as leaf coloration in at least some cultivars of lettuce. Additionally, when UVA and B light were applied at the same PFD as EOP lighting, they were equally effective at increasing TPC, TAC, and leaf coloration. Moreover, EOP light with longer wavelengths (i.e., $G_{20}+R_{40}$ treatment) did not increase TPC, TAC, or leaf redness. More research is needed to determine the most effective peak wavelength and dose (PFD and duration) of light to achieve desired plant outcomes while also considering sustainability, including the technical performance of LEDs. Furthermore, additional research is needed to determine how the background spectrum and PFD interact with EOP lighting treatments.

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