

Blue Radiation Interacts with Green Radiation to Influence Growth and Predominantly Controls Quality Attributes of Lettuce

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ABSTRACT. Adding green [G (500–600 nm)] radiation to blue [B (400–500 nm)] and red [R (600–700 nm)] radiation creates white radiation and improves crop inspection at indoor farms. Although G radiation can drive photosynthesis and elicit the shade-avoidance response, its effects on plant growth and morphology have been inconsistent. We postulated G radiation would counter the suppression of crop growth and promotion of secondary metabolism by B radiation depending on the B photon flux density (PFD). Lettuce (*Lactuca sativa* ‘Rouxai’) was grown in a growth room under nine sole-source light-emitting diode (LED) treatments with a 20-hour photoperiod or in a greenhouse. At the same photosynthetic photon flux density [PPFD (400–700 nm)] of $180 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, plants were grown under warm-white LEDs or increasing B PFDs at 0, 20, 60, and $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with or without substituting the remaining R radiation with $60 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of G radiation. Biomass and leaf expansion were negatively correlated with the B PFD with or without G radiation. For example, increasing the B PFD decreased fresh and dry mass by up to 63% and 54%, respectively. The inclusion of G radiation did not affect shoot dry mass at 0 or $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B radiation, but it decreased it at 60 or $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B radiation. Results suggest that the shade-avoidance response is strongly elicited by low B radiation and repressed by high B radiation, rendering G radiation ineffective at controlling morphology. Moreover, substituting R radiation with G radiation likely reduced the quantum yield. Otherwise, G radiation barely influenced morphology, foliage coloration, essential nutrients, or sensory attributes regardless of the B PFD. Increasing the B PFD increased red foliage coloration and the concentrations of several macronutrients (e.g., nitrogen and magnesium) and micronutrients (e.g., zinc and copper). Consumers preferred plants grown under sole-source lighting over those grown in the greenhouse, which were more bitter and less acceptable, flavorful, and sweet. We concluded that lettuce phenotypes are primarily controlled by B radiation and that G radiation maintains or suppresses lettuce growth depending on the B PFD.

Because of the emerging interest in producing local, fresh, and nutritious food throughout the year, indoor farming has recently been expanding rapidly in urban and peri-urban areas (Kozai et al., 2015). High-value, fast-growing, and short-stature crops, such as leafy greens and herbs, are common crop types that are suitable for commercial indoor vertical farming (Kozai et al., 2015). Light-emitting diodes (LEDs) are the predominant

light source of indoor vertical production systems because they can be placed close to the crop canopy, are energy-efficient and long-lasting, and have customizable spectral distributions (Massa et al., 2008). Because radiation quality influences physiological processes such as photosynthesis, photomorphogenesis, and secondary metabolism, characterizing and understanding crop spectral responses are crucial to achieving desired yield and quality attributes, such as shape, texture, nutritional value, and organoleptic properties. Biologically relevant wavebands delivered by LEDs include ultraviolet (280–400 nm), blue [B (typical peak wavelength, 450 nm)], green [G (typical peak wavelength, 525 nm)], red [R (typical peak wavelength, 660 nm)], and far red [FR (700–800 nm; typical peak wavelength, 735 nm)]. Changing the spectral composition can shift the energy balance to affect quantum efficiency and photoprotective mechanisms involving secondary metabolic compounds (Hogewoning et al., 2012; Kopsell et al., 2015). However, the spectral composition, such as the ratio of R to FR radiation, can evoke the shade-avoidance response to modify morphological traits (Franklin, 2008).

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A typical green leaf of plants grown in growth chambers absorbed $\approx 92\%$ of B radiation (450 nm), 92% of R radiation (660 nm), and 81% of G radiation (525 nm) (McCree, 1972). Radiation transmission and reflection are higher for G radiation than for B or R radiation. Although chlorophylls *a* and *b* on the adaxial leaf surface absorb most B and R radiation and little G radiation, up to 80% of G radiation is transmitted through the mesophyll and penetrates deeper in the leaf profile (Brodersen and Vogelmann, 2010; Terashima et al., 2009). For a wide range of grain, oilseed, vegetable, and other crops grown in growth chambers, the relative quantum yields based on absorbed photons in low light ($\approx 100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were ≈ 0.75 , 0.74 , and 0.93 for B (450 nm), G (525 nm), and R radiation (660 nm), respectively (McCree, 1972; Sager et al., 1988). More recently, quantum yields at various wavelengths were quantified again for cucumber [*Cucumis sativus* (Hogewoning et al., 2012)]. In low light, the quantum yield based on absorbed photons was highest for R radiation, followed by G radiation and then B radiation, whereas the quantum yield based on incident photons was the highest for R radiation and similarly lower for B and G radiation [$\approx 70\%$ of the highest yield (Hogewoning et al., 2012)]. The quantum yield under absorbed G radiation was higher than that under B radiation because of the deeper penetration of G radiation in the mesophyll and its prolonged light paths in the leaf through scattering (Smith et al., 2017). Therefore, G radiation drives photosynthesis effectively despite its relatively weak absorption by chlorophylls and widely misconceived low quantum efficiency. The spectral composition in the background and spectra need to be clearly defined when evaluating the effects of additional G radiation on photosynthesis. For example, in theory, substituting incident B radiation with G radiation would not change the quantum yield, whereas substituting incident R radiation with G radiation would decrease it.

A low ratio of R to FR radiation, low B radiation, and inclusion of G radiation can trigger the shade-avoidance response, such as promotion of extension growth, acceleration of flowering, and hyponasty (Keuskamp et al., 2011; Smith and Whitelam, 1997; Zhang et al., 2011). The shade-avoidance response is mediated by phytochromes, such as phytochrome B, at a low ratio of R to FR radiation, by cryptochromes 1 and 2 in low B radiation, and through a less understood mechanism in the presence of G radiation (Pedmale et al., 2016; Smith and Whitelam, 1997; Zhang et al., 2011). Increased leaf expansion under shade signals such as a low ratio of R to FR radiation can increase radiation capture, thereby promoting whole-plant photosynthesis (Park and Runkle, 2017). Many shade-induced genes upregulated by FR radiation can also be activated by G radiation, although suppression of gene expression by cryptochromes in G radiation occurs without FR radiation (Zhang et al., 2011). At the whole-plant level, at a photosynthetic photon flux density (*PPFD*) of $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, substituting $36 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of R radiation with G radiation at a B photon flux density (*PF*) of $23\text{--}24 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ promoted leaf expansion and biomass accumulation of ‘Waldmann’s Green’ lettuce (Kim et al., 2004). However, other studies suggested minimal roles of G radiation in plant growth and morphology. For example, at a *PPFD* of $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, substituting R in B+R radiation with $15 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of G radiation generally did not influence leaf shape or biomass of ‘Green Skirt’ lettuce when the B *PPFD* was 0, 15, 30, or $45 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Kang et al., 2016). In addition, at a low B fraction of 10% to 14%, increasing the G radiation fraction from

0% to 41% did not influence the shoot dry mass of ‘Waldmann’s Green’ lettuce at a *PPFD* of 200 or $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; however, it decreased its leaf area index by 11% at a *PPFD* of $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, but not $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Snowden et al., 2016). These inconsistent findings regarding G radiation necessitate a detailed investigation that eliminates possible confounding factors to elucidate spectral interactions.

Energetic B photons can elicit the accumulation of essential nutrients and secondary metabolites that have nutritional value and impart flavor (Kopsell et al., 2015; Son and Oh, 2013). For example, increasing the B *PF* (or fraction) increased concentrations of total phenolics and flavonoids and promoted the antioxidant capacity of ‘Sunmang’ lettuce and ‘Grand Rapids TBR’ lettuce (Son and Oh, 2013). Partial substitution of white radiation with B radiation increased concentrations of anthocyanins, xanthophylls, and β -carotenes of ‘Red Cross’ lettuce (Li and Kubota, 2009). Increases in anthocyanins by high B radiation can be attributed to the increased activity of phenylalanine ammonia-lyase, a key enzyme in the biosynthetic pathways of polyphenol compounds (Heo et al., 2012). Because secondary metabolites such as phenolic compounds are bitter (Tomás-Barberán and Espín, 2001), B radiation can potentially affect consumer preferences of organoleptic properties. However, few studies of LED lighting have investigated spectral regulation of crop flavor and texture. In one study, compared with B+R radiation, B+R+white radiation and white fluorescent light improved sensory attributes, such as shape, color, sweetness, and crisp texture, of ‘Capitata’ lettuce, suggesting the influence of G radiation (Lin et al., 2013).

In a previous study, substituting $60 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B radiation with G radiation in a background of $120 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of R radiation increased biomass accumulation and extension growth of ‘Rex’ lettuce, ‘Rouxai’ lettuce, and kale (*Brassica oleracea* var. *sabellica* ‘Siberian’) (Meng et al., 2019). However, because the B *PF* decreased with incremental additions of G radiation, the promotion of plant growth under enriched G radiation could also be attributed to reduced B radiation. In the present study, to decouple the effects of G radiation from those of B radiation, R radiation was partially substituted with G radiation at various B *PPFD*s in the present study. In addition, indoor vertical farms and greenhouses are two major systems for producing crops in controlled environments, but few studies have compared their crop yield and quality. Therefore, we compared lettuce growth and quality in a growth room under sole-source lighting and in a greenhouse environment under sunlight with supplemental lighting. For ‘Rouxai’ red leaf lettuce, we postulated that 1) increasing the B *PPFD*, with or without G radiation, would decrease leaf expansion and biomass, increase the accumulation of anthocyanins, macronutrients, and micronutrients, and intensify the bitter taste; 2) partial substitution of R radiation with G radiation would counter the effects of B radiation in a B *PPFD*-dependent manner and elicit the shade-avoidance response, thereby increasing radiation interception and biomass; and 3) plant growth under sole-source lighting with low B radiation would be greater than that in a greenhouse environment with moderate B radiation from sunlight because increasing B radiation would reduce vegetative growth.

Materials and Methods

PLANT MATERIAL AND PROPAGATION. This study was conducted in the Controlled-Environment Lighting Laboratory at

Michigan State University (East Lansing). Seeds of 'Rouxai' red oakleaf lettuce were obtained from a seed producer (Johnny's Selected Seeds, Winslow, ME) and sown in a rockwool substrate sheet composed of 200 2.5-cm-wide square plugs (AO 25/40 Starter Plugs; Grodan, Milton, ON, Canada) on 11 Jan. and 19 Feb. 2018 for two replications. The substrate was held in a plastic tray and presoaked in deionized water with an adjusted pH of 4.3 using diluted (1:31) 95% to 98% sulfuric acid (J.Y. Baker, Phillipsburg, NJ). During the first 24 h, seed trays were covered with transparent humidity domes and placed in a growth room at 20 °C under continuous lighting from warm-white LEDs (2700 K, PHYTOFY RL; Osram, Beverley, MA) at a total photon flux density [*TPFD* (400–800 nm)] of 50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. On day 1, the air temperature, photoperiod, and *TPFD* were changed to 22 °C, 20 h, and 180 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. The substrate was subirrigated with a nutrient solution [pH, 5.7–5.9; electrical conductivity (EC), 1.2–1.4 $\text{mS}\cdot\text{cm}^{-1}$] to supply the following nutrients (in $\text{mg}\cdot\text{L}^{-1}$): 125 N, 18 P, 139 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 nutrient solution used from days 1 to 13 was made by supplementing deionized water with 12N–1.7P–13.3K water-soluble fertilizer (RO Hydro FeED; JR Peters, Allentown, PA) and magnesium sulfate (Epsom salt; Pennington Seed, Madison, GA). The pH was adjusted to the desired range by the addition of potassium bicarbonate and/or diluted sulfuric acid.

LIGHTING TREATMENTS. On day 4, after humidity domes were removed, 35 lettuce seedlings were transferred from warm-white radiation to each of nine light-quality treatments at the same *TPFD* of 180 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under a 20-h photoperiod. Plants were exposed to four B *PF*Ds in an R background without G radiation (R_{180} , $B_{20}R_{160}$, $B_{60}R_{120}$, and $B_{100}R_{80}$) or with the substitution of G radiation for R radiation ($G_{60}R_{120}$, $B_{20}G_{60}R_{100}$, $B_{60}G_{60}R_{60}$, and $B_{100}G_{60}R_{20}$). The number following each waveband is its *PF*D in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Additional plants were kept under warm-white radiation. The peak wavelengths of B, G, R, and warm-white LEDs included in each LED fixture (PHYTOFY RL; Osram) were 449, 526, 664, and 639 nm, respectively. The LED hardware was paired with software (PHYTOFY Control Software; Osram) to create the lighting treatments and schedules. Each lighting treatment was delivered with an array of three identical LED fixtures (67.3 × 29.8 × 4.3 cm each, placed 41 cm apart), and their color channels were controlled to deliver the desired spectral distributions. Before the onset of each replication, spectra were measured with a portable spectroradiometer (PS200; Apogee Instruments, Logan, UT) at the plant canopy (46 cm below the LED fixtures) and averaged from seven locations for each lighting treatment to create an average spectral distribution (Fig. 1). Single-band *PF*Ds for B, G, R, and FR radiation, integrated *PF*Ds (e.g., *TPFD* and *PPFD*), and radiation ratios were calculated based on the average spectral distribution (Table 1). The yield photon flux density [*YPPFD* (300–800 nm)] was the product of the spectral distribution and relative quantum yield according to Sager et al. (1988). The phytochrome photoequilibrium describes the fraction of FR-absorbing phytochromes in the total phytochrome pool and was estimated based on the spectral distribution and phytochrome absorption coefficients (Sager et al., 1988). The color rendering index, which measures how well a light source reveals object colors compared with a natural light source, was calculated with the online LED ColorCalculator (Osram Sylvania Inc., 2019).

The photosynthetic daily light integral [DLI (400–700 nm)] was 13.0 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$.

PRODUCTION CULTURE AND ENVIRONMENT. On day 13, lettuce seedlings were transplanted to a deep-flow technique hydroponic system on three-layer growing racks (Indoor Harvest, Houston, TX) in the same radiation and temperature environment as before. Plants were positioned on 36-cell floating rafts [60.9 × 121.9 × 2.5 cm (Beaver Plastics, Acheson, AB, Canada)] in flood tables [1.22 × 0.61 × 0.18 m (Active Aqua AAHR24W; Hydrofarm, Petaluma, CA)]. A nutrient solution was constantly recirculated by a water pump in a reservoir and oxygenated by an air stone [20.3 × 2.5 cm (Active Aqua AS8RD; Hydrofarm)] connected to an air pump (Active Aqua AAPA70L; Hydrofarm). It was made of deionized water supplemented with 12N–1.7P–13.3K water-soluble fertilizer (RO Hydro FeED) and potassium bicarbonate to supply the following nutrients (in $\text{mg}\cdot\text{L}^{-1}$): 150 N, 22 P, 166 K, 88 Ca, 58 Mg, 47 S, 2.1 Fe, 0.63 Mn, 0.68 Zn, 0.15 B, 0.56 Cu, and 0.15 Mo. The pH, EC, and water temperature for each rack housing three lighting treatments were measured daily with a pH and EC meter (HI9814; Hanna Instruments, Woonsocket, RI). The pH, EC, and water temperature of nutrient solutions for nine sole-source lighting treatments were (mean ± SD) 5.9 ± 0.5 to 5.9 ± 0.7, 1.76 ± 0.12 to 1.80 ± 0.16 $\text{mS}\cdot\text{cm}^{-1}$, and 23.1 ± 0.3 to 24.0 ± 0.7 °C in replication 1, and 5.5 ± 0.5 to 5.8 ± 0.7, 1.77 ± 0.10 to 1.83 ± 0.08 $\text{mS}\cdot\text{cm}^{-1}$, and 23.1 ± 0.2 to 23.9 ± 0.2 °C in replication 2. When pH decreased to <5.1, it was increased to 5.6–5.9 using potassium bicarbonate. The nutrient solution tank was replenished with deionized water before the water pump surfaced. No additional fertilizers were added throughout the experiment. The *PPFD*, air temperature, CO₂ concentration, and relative humidity were monitored with sensors and recorded as described by Meng et al. (2019). The mean air temperature, CO₂ concentration, and relative humidity in the growth room were (mean ± SD) 22.4 ± 0.6 °C, 410 ± 50 $\mu\text{mol}\cdot\text{mol}^{-1}$, and 34% ± 10%, respectively, in replication 1 and 22.5 ± 0.6 °C, 398 ± 35 $\mu\text{mol}\cdot\text{mol}^{-1}$, and 35% ± 7%, respectively, in replication 2.

Additional lettuce seedlings grown under warm-white radiation were transferred on day 13 to a glass-glazed greenhouse at 22 °C with an environmental control system (Integro 725; Priva, De Lier, The Netherlands). During a 16-h photoperiod (different from 20 h indoors to achieve comparable DLIs), supplemental lighting from high-pressure sodium lamps (PL2000; P.L. Light Systems, Beamsville, ON, Canada) was automatically switched on to provide an additional *PPFD* of 60–90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height when the ambient *PPFD* was <185 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and switched off when it was >370 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Supplemental lighting was manually turned off on day 23 in replication 2 because of an overabundance of sunlight. Supplemental lighting contributed ≈22% and 13% of the DLIs during replications 1 and 2, respectively. Plants were transplanted to 10-cm plastic pots filled with a peat-perlite medium (Suremix; Michigan Grower Products, Galesburg, MI) and irrigated using an overhead watering can filled with reverse-osmosis water supplemented with the same 12N–1.7P–13.3K fertilizer (RO Hydro FeED) at the same nutrient concentrations as that for plants in the growth room. The initial pH and EC of the nutrient solution were 5.6 and 1.6 $\text{mS}\cdot\text{cm}^{-1}$, respectively. The pH was maintained at ≈5.6 using potassium bicarbonate throughout the experiment. An IR thermocouple (OS36-01-K-80F; Omega Engineering, Stamford, CT) and a line quantum sensor (Apogee Instruments) were used to mea-

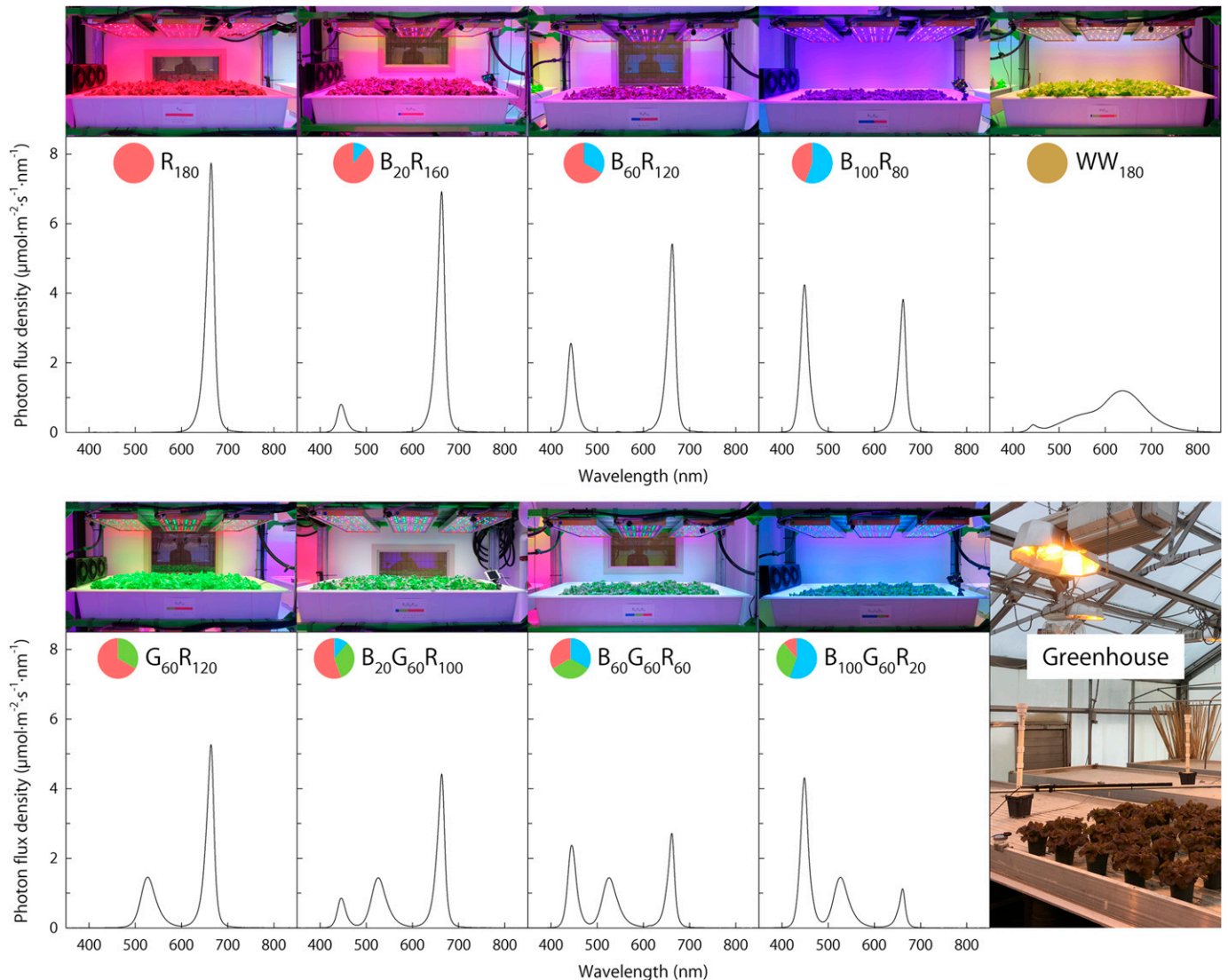


Fig. 1. Spectral distributions of nine sole-source lighting treatments delivered by mixtures of blue [B (400–500 nm)], green [G (500–600 nm)], and red [R (600–700 nm)], or warm-white (WW) light-emitting diodes. The greenhouse treatment received sunlight with supplemental high-pressure sodium lighting. The number following each waveband is its photon flux density in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

sure leaf temperature and the *PPFD*, respectively, at plant height. Hourly average data were calculated from instantaneous measurements every 10 s with a data logger (CR10; Campbell Scientific, Logan, UT). The mean leaf temperature and DLI were (mean \pm SD) 21.8 ± 2.3 °C and 15.9 ± 3.4 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively, in replication 1 and 22.7 ± 2.2 °C and 19.2 ± 4.9 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively, in replication 2.

DATA COLLECTION AND ANALYSIS. On day 33 in replication 1 and day 30 in replication 2, growth data were collected from eight plants per treatment for destructive measurements. The harvest times of two replications were different by 3 d to accommodate subsequent prescheduled sensory tests. Shoot fresh and dry mass following ≥ 5 d in a drying oven (Blue M, Blue Island, IL) at 60 °C were measured with an analytical balance (GX-1000; A&D Store, Wood Dale, IL). Plant diameter (the longest horizontal distance between leaf peripheries), leaf length and width of the sixth true leaf, and leaf number (when > 3 cm) were measured with a ruler. Relative specific chlorophyll content (SPAD index) was measured with a chlo-

rophyll meter (SPAD-502; Konica Minolta Sensing, Tokyo, Japan). The average SPAD index of each plant was obtained from three measurements at three randomly selected locations on recently matured leaves outside leaf midribs, veins, and margins. Foliage coloration was quantified with a portable colorimeter (Chroma Meter CR-400; Konica Minolta Sensing) as the International Commission on Illumination $L^*a^*b^*$ color space coordinates. L^* indicates leaf brightness, which ranges from 0 (darkest black) to 100 (brightest white). The positive directions of a^* and b^* indicate redness and yellowness, respectively, whereas their negative directions indicate greenness and blueness, respectively. The maximum quantum efficiency of photosystem II (Fv/Fm) was measured on dark-adapted leaves (for 30 min) with a multimode chlorophyll fluorometer (OS5p; Opti-Sciences, Hudson, NH).

Consumer sensory tests were performed at the Sensory Evaluation Laboratory of the Department of Food Science and Human Nutrition at Michigan State University based on the protocol described by Szczygiel et al. (2017). The protocol in

Table 1. Spectral characteristics of nine sole-source lighting treatments delivered by mixtures of blue [B (400–500 nm)], green [G (500–600 nm)], and red [R (600–700 nm)], or warm-white (WW) light-emitting diodes (LEDs).^z

	LED lighting treatment								
	R ₁₈₀	G ₆₀ R ₁₂₀	B ₂₀ R ₁₆₀	B ₂₀ G ₆₀ R ₁₀₀	B ₆₀ R ₁₂₀	B ₆₀ G ₆₀ R ₆₀	B ₁₀₀ R ₈₀	B ₁₀₀ G ₆₀ R ₂₀	WW ₁₈₀
	Single-band photon flux density ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)								
B	0.1	3.4	19.6	24.3	58.6	62.1	99.6	103.1	12.1
G	0.5	60.7	0.8	58.9	1.0	58.8	0.7	60.1	51.9
R	180.1	120.8	158.9	99.1	121.9	57.5	83.1	23.2	98.4
FR	1.6	1.5	1.8	1.2	1.3	0.7	0.8	0.4	18.6
	Integrated photon flux density ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)								
PPFD	180.7	185.0	179.3	182.3	181.6	178.4	183.4	186.3	162.4
TPFD	182.3	186.5	181.1	183.5	182.9	179.1	184.2	186.7	181.0
YPPFD	167.7	162.8	163.1	156.5	158.2	146.1	151.8	145.4	148.9
	Radiation ratio								
B:R	0.0	0.0	0.1	0.2	0.5	1.1	1.2	4.5	0.1
B:G	0.2	0.1	25.6	0.4	58.4	1.1	137.9	1.7	0.2
G:R	0.0	0.5	0.0	0.6	0.0	1.0	0.0	2.6	0.5
R:FR	111.2	80.6	86.8	85.5	91.9	84.6	103.7	57.5	5.3
PPE	0.883	0.882	0.880	0.876	0.869	0.855	0.855	0.796	0.828
	Visual quality								
CRI	42	38	-58	58	-250	61	-222	51	97

^zThe number following each waveband is its photon flux density in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Photon flux densities over 1-nm increments were integrated as the photosynthetic photon flux density [PPFD (400–700 nm)] and the total photon flux density [TPFD (400–800 nm)], which includes far-red [FR (700–800 nm)] radiation. The yield photon flux density [YPPFD (300–800 nm)] was the product of the spectral distribution and relative quantum efficiency (Sager et al., 1988). The phytochrome photoequilibrium (PPE) was estimated according to Sager et al. (1988). The color-rendering index (CRI) was calculated based on the spectral distribution using the online LED ColorCalculator (OSRAM Sylvania, 2019).

this study was approved by the Institutional Review Board of Michigan State University. On day 36 in replication 1 and day 32 in replication 2, organoleptic properties of lettuce leaves from six treatments (R₁₈₀, B₂₀R₁₆₀, B₂₀G₆₀R₁₀₀, B₁₀₀R₈₀, B₁₀₀G₆₀R₂₀, and greenhouse) were evaluated by 86 and 78 sensory panelists of older than 18 years, respectively, who consumed lettuce at least once per month. A sensory analysis allowed testing of a limited number of treatments to achieve high-quality results without panelist fatigue. The six treatments were selected for sensory and nutrient analyses because they represented key interactions between B and G radiation and provided for a comparison between the growth room and the greenhouse. The panelists were recruited using the Michigan State University Paid Research Pool by Sona Systems, Ltd. (Tallinn, Estonia). Each panelist was presented with six coded samples in random order and was asked to rate the overall acceptability, appearance, color, texture, overall flavor, and aftertaste using a 9-point hedonic scale, where 1 = dislike extremely and 9 = like extremely. The levels of bitterness and sweetness were measured using a 5-point Likert scale, where 1 = not at all bitter (or sweet) and 5 = extremely bitter (or sweet). How the samples met the expectations of red-leaf lettuce was measured using a 5-point Likert scale, where 1 = much worse than expected and 5 = much better than expected. Willingness to buy was measured using a 5-point Likert scale, where 1 = definitely would not purchase and 5 = definitely would purchase. Subsequently, panelists were asked their age, gender, and consumption frequencies of lettuce, cruciferous vegetables, and coffee.

An elemental analysis was conducted at the U.S. Department of Agriculture Agricultural Research Service (Toledo, OH) for

lettuce leaf tissues from the same six treatments as those used for the sensory analysis. Dry tissues were ground using a mortar and pestle. Foliar nitrogen content was measured with a CHN analyzer (vario MICRO cube; Elementar, Hanau, Germany) using ≈ 2.5 mg dry lettuce tissue in tin capsules (EA Consumables, Pennsauken, NJ). Other macronutrients and micronutrients were quantified with inductively coupled plasma optical emission spectrometry (iCAP 6300 Duo ICP-OES Analyzer; Thermo Fisher Scientific, Waltham, MA) based on the modified U.S. Environmental Protection Agency method 3051 with an extra hydrogen peroxide step. Spinach (*Spinacia oleracea*) leaves [National Institute of Standards and Technology (NIST) standard reference material 1570a] were included for every 20 samples. Peach (*Prunus persica*) leaves (NIST standard reference material 1547) were included for every 40 samples. Five milliliters of nitric acid was combined with ≈ 0.25 g dry lettuce tissue in a polytetrafluoroethylene-based vessel (Teflon; The Chemours Co.,

Wilmington, DE). Samples were placed in a microwave for digestion (MARS 6; CEM Corp., Matthews, NC); the temperature was increased to 200 °C within 15 min, maintained at 200 °C for 15 min, and then decreased to room temperature. After the addition of 1.5 mL of hydrogen peroxide to each sample, samples were reheated to 200 °C and remained at that temperature for 5 min; then, they were cooled to room temperature. Samples were filtered (Whatman qualitative filter paper, Grade 2; Whatman, Maidstone, UK) after the addition of 12 mL of 18 M Ω water to each sample. A 1.3-mL aliquot of the solution was diluted with 8.7 mL of 18 M Ω water for the elemental analysis in the ICP-OES analyzer.

The experiment was performed twice and followed a randomized complete block design. All data were pooled from two replications because the treatment \times replication interaction was not significant ($P > 0.05$) or the response trends were similar between replications. Data were analyzed using SAS (version 9.4; SAS Institute, Cary, NC) with the PROC MEANS, PROC MIXED, and PROC GLIMMIX procedures and Tukey's honestly significant difference test ($\alpha = 0.05$). Photographs of a representative plant from each treatment were obtained to show visual differences (Fig. 2).

Results

BIOMASS. Irrespective of the presence of G radiation, there were linear negative relationships between the B PFD and biomass accumulation. At a PPF of 180 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, increasing the B PFD from 0 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ decreased shoot fresh and dry mass by 58% and 46%, respectively, in an R radiation

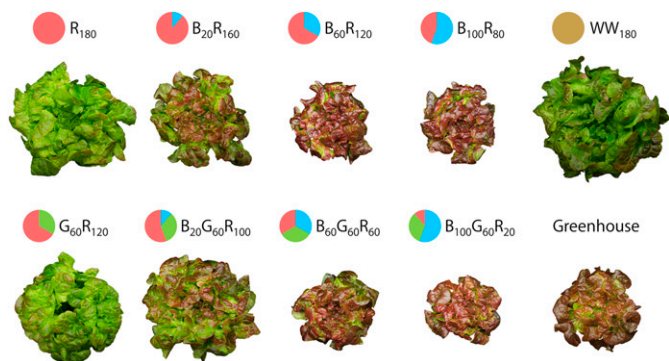


Fig. 2. 'Rouxai' lettuce 32 d after sowing from the first replication. Plants were grown under nine sole-source lighting treatments delivered by mixtures of blue [B (400–500 nm)], green [G (500–600 nm)], and red [R (600–700 nm)], or warm-white (WW) light-emitting diodes or a greenhouse treatment that received sunlight supplemented with high-pressure sodium lighting. The number following each waveband is its photon flux density in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

background and by 63% and 54%, respectively, with 60 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of G radiation as substitution of R radiation (Fig. 3). The effects of G radiation varied depending on the B *PPFD*. G radiation did not influence the shoot fresh mass when B radiation was absent, increased it by 18% at B_{20} , and decreased it by 29% and 19% at B_{60} and B_{100} , respectively. G radiation did not influence the shoot dry mass at B_0 or B_{20} , but it decreased it by 26% and 20% at B_{60} and B_{100} , respectively. The shoot fresh or dry mass was similar under WW_{180} and $G_{60}R_{120}$. Plants grown in the greenhouse had shoot fresh and dry mass comparable to those grown under $B_{100}R_{80}$, although they received higher DLIs.

MORPHOLOGY. Increasing the B *PPFD* in the presence of G radiation decreased leaf length linearly by up to 17% (Fig. 3). Without G radiation, leaf length decreased by 13% from B_0 to B_{20} , but it did not change beyond B_{20} . Substituting R radiation with G radiation did not affect leaf length at any B *PPFD* delivered. Plants grown under WW_{180} and in the greenhouse had leaf length similar to those grown under R_{180} and $G_{60}R_{120}$. Increasing the B *PPFD* from 0 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ decreased leaf width by 34% and 29% with and without G radiation, respectively. Leaf width was similar with or without G radiation at B_0 , B_{20} , and B_{60} , but it was 9% lower with G radiation at B_{100} . Leaves were widest under R_{180} , $G_{60}R_{120}$, and WW_{180} ; they were narrowest under $B_{100}G_{60}R_{20}$ and in the greenhouse. Plant diameter decreased linearly with an increasing B *PPFD* by up to 21% with G radiation and 18% without G radiation. G radiation decreased plant diameter by 9% at B_{60} , but it did not affect it at the other B *PPFDs*. Without G radiation, plants had two or three more leaves at B_0 than at B_{20} and B_{100} . In the presence of G radiation, plants developed three more leaves at B_0 and B_{20} (and under WW_{180}) than at B_{60} and B_{100} (and in the greenhouse). Substituting G radiation for R radiation increased leaf number by three at B_{20} , but not at the other B *PPFDs*.

SPAD AND Fv/Fm. With or without G radiation, increasing the B *PPFD* from 0 to 20 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased the SPAD index by 12% to 13% and saturated this response (Fig. 3). The inclusion of G radiation decreased the SPAD index by 9% at B_{60} , but not at the other B *PPFD*. Increasing the B *PPFD* from 0 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ did not affect Fv/Fm in the absence of G radiation, but it increased it by 3% in the presence of G radiation. Fv/Fm was similar under WW_{180} and at B_0 and B_{20} , and it was similar in the greenhouse and at B_{100} .

FOLIAGE COLORATION. With or without G radiation, increasing the B *PPFD* from 0 to 20 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ decreased brightness (L^*) and yellowness (b^*) and increased redness (a^*) of foliage directly exposed to radiation (Figs. 2 and 4). Colors generally saturated with 20 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B radiation; however, in the presence of G radiation, foliage redness saturated at 60 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B radiation. Substituting G radiation for R radiation did not influence foliage coloration at any B *PPFD*. Foliage coloration of plants grown under WW_{180} , which included B_{12} , was between that of the B_0 and B_{20} treatments. Plants grown in the greenhouse had foliage coloration similar to those grown at $B_{100}R_{80}$.

SENSORY ATTRIBUTES. Regardless of differences in leaf color, plant appearance and color were rated similarly by panelists across all tested treatments (Fig. 5). Substituting G radiation for R radiation did not influence any sensory attribute at B_{20} or B_{100} . Ratings of overall acceptability, flavor, aftertaste, meeting expectations, and willingness to buy were 9% to 13%, 15% to 18%, 15% to 17%, 13% to 19%, and 15% to 20% lower, respectively, for greenhouse-grown plants than for plants grown under the five sole-source lighting treatments. These sensory attributes were similar under the five sole-source lighting treatments. Leaf texture was rated 6% lower under $B_{100}G_{60}R_{20}$ than under R_{180} . Bitterness of greenhouse-grown plants was rated 37% to 50% higher than that under the five sole-source lighting treatments. In the absence of G radiation, increasing the B *PPFD* from 0 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ decreased the sweetness rating by 14%. Sweetness was rated similarly low for plants grown in the greenhouse and under $B_{100}G_{60}R_{20}$.

ESSENTIAL NUTRIENTS. There were no treatment effects on phosphorus, calcium, iron, and boron concentrations (Fig. 6). Substituting G radiation for R radiation at B_{20} or B_{100} did not affect any macronutrient or micronutrient concentrations. In the absence of G radiation, increasing the B *PPFD* from 0 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased nitrogen, magnesium, sulfur, zinc, and copper concentrations by 15%, 10%, 19%, 19%, and 45%, respectively, but it did not affect the other nutrient concentrations. With G radiation, increasing the B *PPFD* from 20 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased nitrogen and sulfur concentrations by 10% and 29%, respectively, but it did not influence the other nutrient concentrations. Plants grown in the greenhouse were 22% to 26%, 44% to 54%, and 61% to 70% lower in potassium, manganese, and molybdenum concentrations, respectively, and 36% to 71% higher in magnesium concentration compared with those grown under five sole-source lighting treatments. The nitrogen concentration in greenhouse-grown plants was similar to that under R_{100} and $B_{20}R_{160}$. The sulfur, zinc, and copper concentrations in greenhouse-grown plants were similar to those under $B_{100}G_{60}R_{20}$.

Discussion

Meng et al. (2019) reported that the incremental substitutions of G radiation for B radiation in $B_{60}R_{120}$ increased the biomass and leaf expansion of 'Rex' lettuce, 'Rouxai' lettuce, and 'Siberian' kale. Similarly, substituting 14 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of G radiation for B_{42} or B_{60} in an R radiation background increased fresh and dry mass and leaf area of 'Sunmang' red-leaf lettuce (Son and Oh, 2015). However, because B radiation was not kept constant, increased plant growth could be attributed to diminishing B radiation rather than increasing G radiation. In the present study, G radiation as substitution of

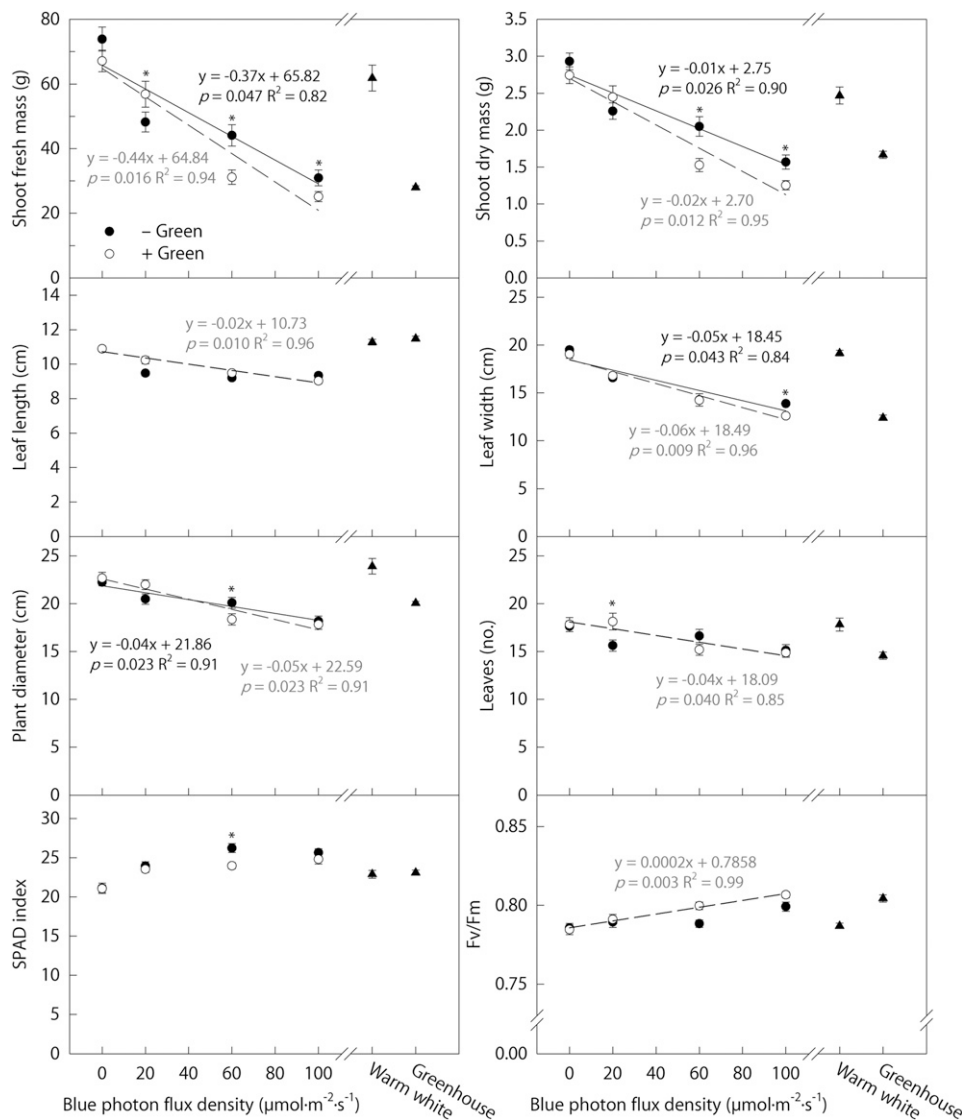


Fig. 3. Shoot fresh and dry mass, leaf length and width, plant diameter, leaf number, the SPAD index, and maximum quantum efficiency of photosystem II (Fv/Fm) of ‘Rouxai’ lettuce grown under nine sole-source lighting treatments, with or without green radiation, or in a greenhouse. Equations, P values, and coefficients of determination (R^2) are given for linear responses to the blue photon flux density ($\alpha = 0.05$) with green radiation (solid lines and black text) and without green radiation (dashed lines and gray text). At any blue photon flux density, an asterisk indicates means with and without green radiation are significantly different based on Tukey’s honestly significant difference test ($\alpha = 0.05$). Error bars show SE.

R radiation had variable effects at multiple fixed B $PPFD$ s. In the absence of B radiation, G radiation did not influence any parameters measured. Under low B radiation (B_{20}), G radiation increased the shoot fresh mass and leaf number. Under moderate B radiation (B_{60}), G radiation decreased the shoot fresh and dry mass, plant diameter, and SPAD index. Under high B radiation (B_{100}), G radiation decreased the shoot fresh and dry mass and leaf width. This interaction between B and G radiation is a novel discovery that adds complexity to spectral responses in plants, although the changing R $PPFD$ could also be part of the interaction. A similar study confirmed that increasing the B $PPFD$ from 0 to $45 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ decreased lettuce growth and leaf expansion, but there were no effects of $15 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of G radiation at the B $PPFD$ s tested (Kang et al., 2016). In comparison, the dependence of G radiation effects on the B

$PPFD$ was found in our study using a wider range of B $PPFD$ s (between 0 and $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and higher G $PPFD$ ($60 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

The minimal effects of G radiation under low B radiation were consistent with some previous studies. For example, at a $PPFD$ of $173 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, substituting $17 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of R radiation with G radiation did not influence the biomass and leaf area of ‘Grand Rapids TBR’ lettuce at B_{22} and B_{42} , although it increased those of ‘Sunmang’ lettuce at B_{42} , but not at B_{22} (Son and Oh, 2015). The low G $PPFD$ (G_{17}) was regarded as less effective than a higher one (G_{36}) at promoting growth rates in a quantitative manner; however, the high G $PPFD$ (G_{60}) in our study marginally influenced growth under low B radiation. In addition, G radiation in $B_{20}G_{28}R_{52}$ was interpreted as neither promotive nor inhibitory for the growth and morphology of cucumber ‘Cumlaude’ because the data fit the dose-response relationships with the B $PPFD$, although $B_{20}R_{80}$ was not provided as a direct comparison (Hernández and Kubota, 2016). Similarly, under low B radiation ($21\text{--}28 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), increasing the G $PPFD$ from 3 to $82 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at a $PPFD$ of $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ did not affect dry mass or net assimilation of ‘Waldmann’s Green’ lettuce (Snowden et al., 2016). Although these findings suggested G radiation neither promoted nor suppressed plant growth, other studies indicated positive or negative roles of G radiation under low B radiation. For example, substituting $36 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of R radiation in $B_{24}R_{126}$ (from LEDs) with G radiation (from filtered fluorescent lamps) in-

creased the leaf area, shoot fresh mass, and shoot dry mass of ‘Waldmann’s Green’ lettuce (Kim et al., 2004); however, these results could be confounded by increases in diffuse radiation or leaf temperature due to the use of green fluorescent lamps (Snowden et al., 2016). On the contrary, substituting G radiation for half the R radiation in R_{160} decreased leaf area and shoot fresh and dry mass of tomato (*Solanum lycopersicum* ‘Early Girl’), salvia (*Salvia splendens* ‘Vista Red’), and petunia (*Petunia xhybrida* ‘Wave Pink’) seedlings, but not impatiens (*Impatiens walleriana* ‘SuperElfin XP Red’) seedlings (Wollaeger and Runkle, 2014). This indicated that different plant species can have various responses to G radiation.

In the present study, at the same $PPFD$, substituting G radiation for R radiation decreased biomass accumulation

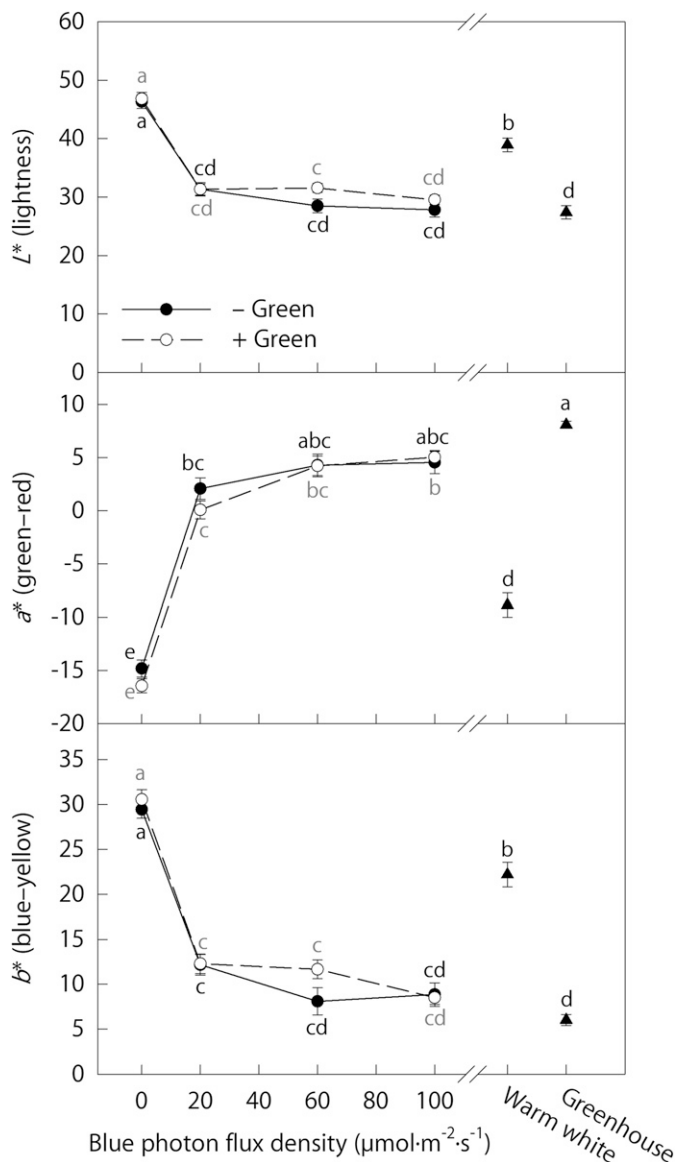


Fig. 4. $L^*a^*b^*$ color space analysis of 'Rouxai' lettuce grown under nine sole-source lighting treatments, with or without green radiation, or in a greenhouse. L^* indicates lightness, ranging from 0 (the darkest black) to 100 (the brightest white). a^* indicates redness in the positive direction and greenness in the negative direction. b^* indicates yellowness in the positive direction and blueness in the negative direction. Means followed by different letters within each parameter are significantly different based on Tukey's honestly significant difference test ($\alpha = 0.05$). Black and gray letters are associated with filled circles (without green radiation) and empty circles (with green radiation), respectively. Error bars show SE.

under moderate to high B radiation. This could be explained, at least partly, by photosynthetic differences. Substituting $15 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of G radiation for R radiation at a $PPFD$ of $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ decreased the photosynthetic rate of 'Green Skirt' lettuce at B_{15} , B_{30} , and B_{45} (but increased it at B_0), although it did not affect leaf shape or plant growth (Kang et al., 2016). However, the photosynthetic rate of 'Waldmann's Green' lettuce was similar with and without G radiation at B_{24} (Kim et al., 2004). In our study, substituting $60 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of G radiation for R radiation decreased the $YPFD$ at B_0 , B_{20} , B_{60} , and B_{100} by 3%, 4%, 8%, and 4%, respectively. Therefore, less

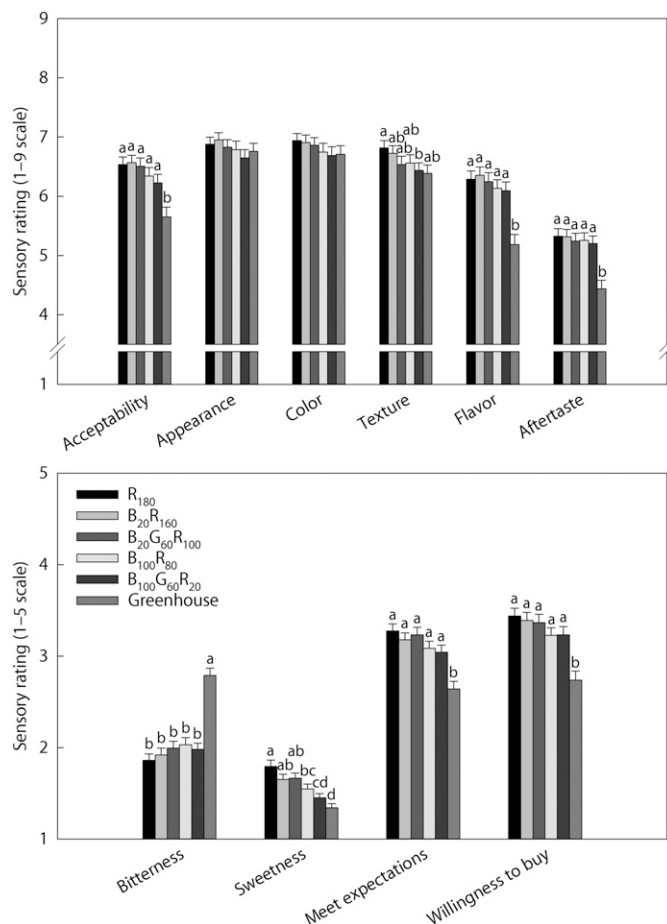


Fig. 5. Sensory ratings of 'Rouxai' lettuce by 164 panelists (86 and 78 in two replications). The upper panel shows sensory ratings on a scale of 1 (dislike extremely) to 9 (like extremely). The lower panel shows sensory ratings on a scale of 1 (low) to 5 (high). Plants were grown under five sole-source lighting treatments or in a greenhouse. The number for each waveband {blue [B (400–500 nm)], green [G (500–600 nm)], or red [R (600–700 nm)]} is its photon flux density in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Means followed by different letters within each category are significantly different based on Tukey's honestly significant difference test ($\alpha = 0.05$). Error bars show SE.

biomass with G radiation at B_{60} can be attributed to a lower $YPFD$, as well as reduced plant diameter and chlorophyll content, which reduced both radiation interception and photosynthesis. Growth inhibition under G radiation at B_{100} was mainly associated with reduced leaf width and, thus, radiation interception rather than the small decrease in the $YPFD$, which did not affect shoot dry mass or leaf expansion at B_0 and B_{20} . These results substantiate a previous notion that G radiation, when added to B+R radiation, can negatively influence plant growth (Folta and Maruhnich, 2007; Went, 1957). In contrast, butterhead lettuce grown under $B_{40}R_{160}$ and $B_{67}G_{67}R_{67}$ with a 12-h photoperiod had similar shoot fresh mass, leaf area, and leaf number (Bian et al., 2018). These plants were grown under white fluorescent lamps until day 14 and received lighting treatments at a DLI of $8.6 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ from days 14 to 34. However, in our study, lighting treatments were applied to plants earlier, longer (from day 4 to day 30 or 33), and at a 50% higher DLI , which could cause different responses.

The relative growth rate of a plant is a function of its leaf area ratio and the net assimilation rate (Lambers et al., 2008).

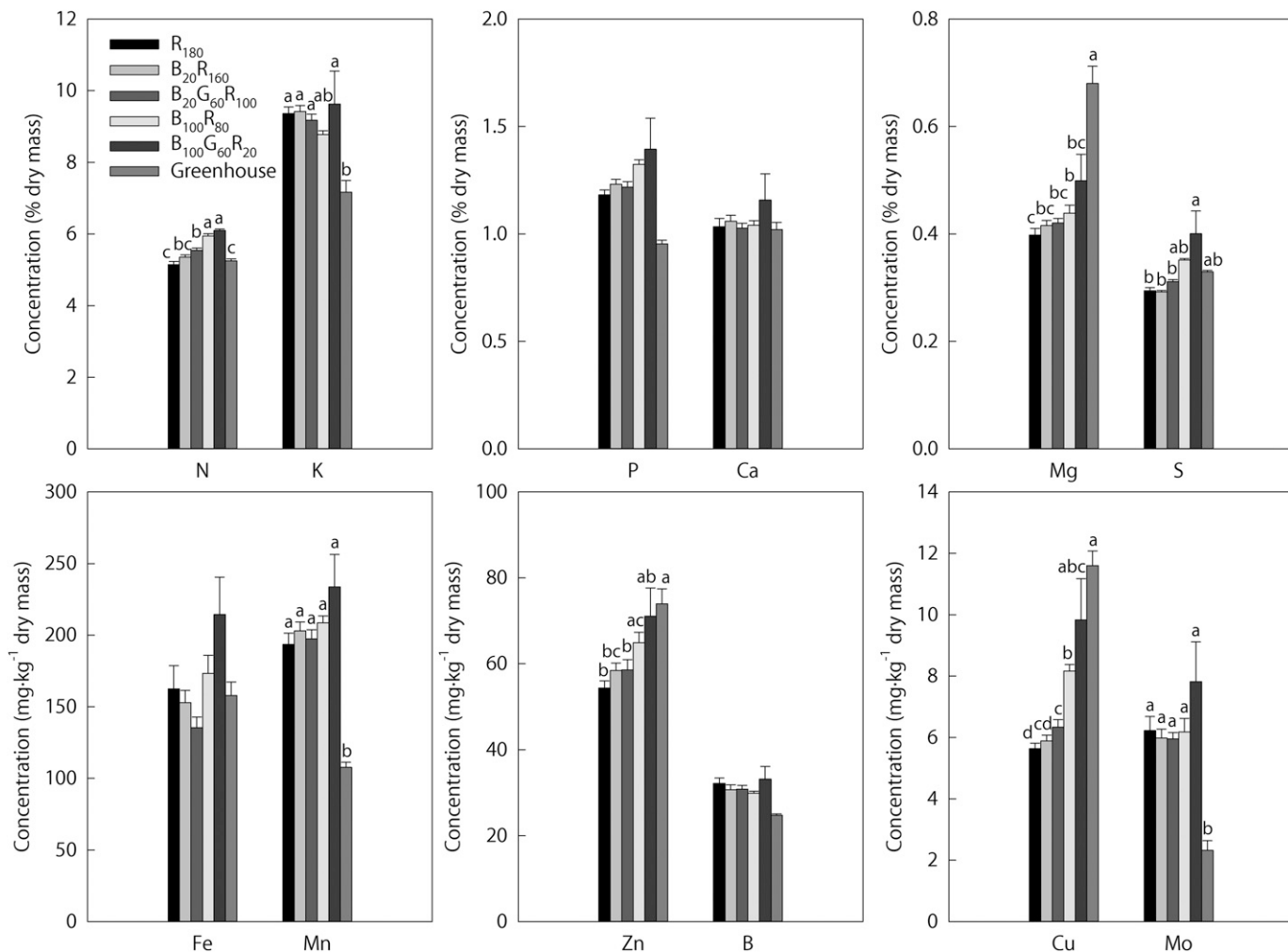


Fig. 6. Concentrations of macronutrients (N, K, P, Ca, Mg, and S) and micronutrients (Fe, Mn, Zn, B, Cu, and Mo) in leaf tissues of 'Rouxai' lettuce. Plants were grown under five sole-source lighting treatments or in a greenhouse. The number for each waveband {blue [B (400–500 nm)], green [G (500–600 nm)], or red [R (600–700 nm)]} is its photon flux density in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Means followed by different letters within each element are significantly different based on Tukey's honestly significant difference test ($\alpha = 0.05$). Error bars show SE.

The leaf area ratio indicates the amount of leaf area available for radiation capture to drive photosynthesis relative to the plant mass. In this study, reduced plant size (i.e., leaf length, leaf width, and plant diameter) was generally associated with reduced biomass accumulation. Increasing the B *PPFD* linearly decreased shoot fresh and dry mass as well as leaf width and plant diameter of 'Rouxai' lettuce, showing B radiation suppression of yield and extension growth. Similarly, incremental substitutions of B radiation for R radiation (from 0 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at a *PPFD* of 171 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) decreased the shoot fresh and dry mass of 'Sunmang' red-leaf lettuce by up to 71% and 61%, respectively, and decreased leaf area by up to 72% (Son and Oh, 2013). In our study, B radiation decreased leaf width more than leaf length, indicating that inhibitory effects of B radiation on leaf expansion were unequal in transverse directions. The observed responses to B radiation in our study can be explained by the roles of cryptochromes in modulating the shade-avoidance response. Plants use photoreceptors, such as cryptochromes, to gauge the incident B *PPFD* (Casal, 2000; Lin, 2000). Extension growth in response to the B *PPFD* is mediated by dynamic, direct interactions between

cryptochromes and phytochrome-interacting factors (PIFs), which are basic helix-loop-helix transcription factors (Pedmale et al., 2016). At a low B *PPFD*, cryptochromes 1 and 2 interact with PIFs 4 and 5 to promote the expression of growth-related genes, whereas at a high B *PPFD*, suppression of PIFs 4 and 5 by cryptochromes and proteasomal degradation of cryptochrome 2 and PIF5 together inhibit extension growth (Pedmale et al., 2016). Reduced B *PPFDs* can elicit the shade-avoidance response, such as stem and hypocotyl elongation and hyponasty, involving the regulation of DELLA proteins through gibberellin, control of auxin, and changes in cell wall extensibility through expansins and xyloglucan endotransglucosylase/hydrolases (Djakovic-Petrovic et al., 2007; Pierik et al., 2004, 2009; Sasidharan et al., 2008).

In most cases, B radiation inhibits stem elongation and leaf expansion; however, the effects of B radiation on extension growth in some studies were inconsistent with this paradigm, possibly because of confounding wavebands, interacting factors, or species- or cultivar-specific sensitivity. For example, using high-pressure sodium and metal halide lamps, increasing the B radiation fraction from 6% to 26% decreased cell

expansion and, thus, leaf expansion in soybean (*Glycine max* ‘Hoyt’); however, increasing the B radiation fraction from 0% to 6% increased cell expansion and division in ‘Grand Rapids’ lettuce (Dougher and Bugbee, 2004). Filter conversion of B radiation to yellow radiation (580–600 nm) to achieve 0% B radiation might be a confounding factor because yellow radiation appeared to suppress lettuce growth (Dougher and Bugbee, 2001). In a subsequent study, changing the B radiation fraction between 11% and 28% did not influence the leaf area index or dry mass of ‘Waldmann’s Green’ lettuce (Snowden et al., 2016), although other wavebands (e.g., G and R radiation) could have confounded the outcomes because B radiation was emitted from broad-spectrum LEDs. Cucumber ‘Cumlaude’ grown under 100% B LEDs at $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ were taller than those grown under R or R+B LEDs and had a greater leaf area than those grown under B₇₅R₂₅ (Hernández and Kubota, 2016). The lack of growth inhibition under 100% B radiation was partly attributed to a low phytochrome photoequilibrium of 0.5 (Hernández and Kubota, 2016); however, 100% B radiation suppressed leaf expansion and decreased the shoot dry mass of lettuce (cultivar unspecified) and ‘Vista Red’ salvia (Wang et al., 2016; Wollaeger and Runkle, 2015). Therefore, atypical sensitivity of specific species and cultivars to B radiation alone is possible.

Although G radiation can elicit the shade-avoidance response (Wang and Folta, 2013; Zhang and Folta, 2012; Zhang et al., 2011), there was no evidence it did so in this study. First, growth and morphological responses to G radiation can change dynamically depending on plant age, which may contribute to some discrepancies in previous studies of plants in different developmental stages. For example, partial substitution of white radiation (B₃₇G₈₆R₅₈) with G radiation (B₃₁G₁₀₄R₄₅) increased the fresh and dry mass and shoot diameter of ‘Outredgeous’ lettuce 14 and 21 d after sowing, but it did not affect the fresh and dry mass or leaf area on day 28 (Mickens et al., 2018). Therefore, plants harvested on days 30 and 33 in our study may be less responsive to G radiation in the maturation phase than in the lag phase. Second, low B radiation is a strong shade signal that may saturate the shade-avoidance response (Keuskamp et al., 2011; Pierik et al., 2004), rendering additional G radiation futile in morphological control. Third, the predominant suppression of extension growth by high B radiation may override weaker control of extension growth by G radiation. For example, leaf area, shoot fresh mass, or shoot dry mass of ‘SuperElfin XP Red’ impatiens, ‘Vista Red’ salvia, or ‘Wave Pink’ petunia seedlings was similar under B₁₆₀ and B₈₀ (Wollaeger and Runkle, 2014).

Taken together with antagonism between B and G radiation with fixed R radiation reported by Meng et al. (2019), the effects of G radiation depend on the specific spectral context. Without the shade-avoidance response as a confounding factor under moderate or high B radiation, G radiation was evidently less effective than R radiation at promoting lettuce growth. This is supported by observations that G radiation is less effective than R radiation at driving photosynthesis (Hogewoning et al., 2012; Kang et al., 2016; McCree, 1972). Therefore, the comparable effectiveness of G and R radiation with little or no B radiation can be attributed to a strong shade-avoidance signal, which G radiation either sustained or at least did not negate. Morphological adaptation to this signal overrode different photosynthetic efficacies between G and R radiation, resulting in similar whole-plant photosynthesis. Isolating the role of G

radiation in the low B radiation-induced shade-avoidance response warrants further investigation.

Increasing the DLI typically increases the shoot dry mass of lettuce (Both et al., 1997; Kitaya et al., 1998). However, shoot dry mass was similarly low for plants grown under B₁₀₀R₈₀ and in the greenhouse, although the average DLI in the greenhouse was 24% to 53% higher than that in the growth room. Confounding factors in the greenhouse environment may include air movement, radiation quality, radiation intensity (the DLI and fluctuating radiation throughout the day), photoperiod, photoinhibition under high radiation, vapor pressure deficit, and the growing method (hydroponics vs. soilless substrate). These uncontrolled variables should be considered when comparing results of the greenhouse and the growth room.

Anthocyanin accumulation was low in foliage without direct exposure to radiation due to shading from other leaves. The inclusion of B radiation at $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was generally sufficient to saturate top foliage coloration and, thus, anthocyanin accumulation of ‘Rouxai’ lettuce, whereas G radiation did not influence foliage coloration at a fixed B PFD. Similarly, the anthocyanin concentration of ‘Red Cross’ red-leaf lettuce was increased by substituting $130 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B radiation, but not G radiation, for white radiation at $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Li and Kubota, 2009). Compared with R radiation, B radiation or B+R radiation at $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased the anthocyanin concentration of ‘Banchu Red Fire’ red-leaf lettuce (Johkan et al., 2010). In addition, 2-h predawn applications of B radiation at $45 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased anthocyanin concentrations in greenhouse-grown ‘Lollo Rossa’ red-leaf lettuce (Ouzounis et al., 2015). The observed anthocyanin accumulation under B radiation can be explained by the involvement of cryptochromes. In *Arabidopsis thaliana*, cryptochrome 1 mediates anthocyanin accumulation under B radiation by upregulating flavonoid biosynthetic enzymes such as chalcone synthase (Bouly et al., 2007; Christie and Briggs, 2001; Jenkins et al., 1995). Cryptochrome 1 is also responsible for B radiation-induced anthocyanin accumulation in rapeseed (*Brassica napus*) (Chatterjee et al., 2006). Cryptochrome 2 can also regulate anthocyanin production under low B radiation, but not high B radiation, in which cryptochrome 2 undergoes rapid degradation (Christie and Briggs, 2001; Pedmale et al., 2016; Wang et al., 2001).

High light is an environmental stress that can elicit anthocyanin accumulation for protection against photodamage (Page et al., 2012). Acclimation to high light is accompanied by increases in flavonoid biosynthesis transcripts in *Arabidopsis* (Page et al., 2012). Therefore, a high anthocyanin concentration in greenhouse-grown lettuce could be attributed to the high DLI. However, phytonutrients such as anthocyanins, phenolic secondary metabolites, and glucosinolates, which can accumulate under B radiation or high light, impart bitter and astringent tastes to fruits and vegetables while increasing the potential health benefits (Kopsell et al., 2015; Tomás-Barberán and Espín, 2001). Compared with lettuce grown under sole-source lighting, the lower ratings of greenhouse-grown lettuce for acceptability, flavor, aftertaste, and willingness to buy were associated with the higher ratings for bitterness. Consumers are generally averse to bitter plant foods regardless of their health-promoting properties, which presents a dilemma for food producers (Drewnowski and Gomez-Carneros, 2000). However, bitter-tasting lettuce may be tolerable if mixed with other

types of salad greens and dressings. In our study, lettuce grown under sole-source lighting had similar foliage coloration but lower bitterness ratings than the greenhouse counterpart, indicating similar anthocyanin accumulation but higher concentrations of other bitter compounds in the greenhouse-grown lettuce. Therefore, sole-source lighting can enable desirable coloration without negatively affecting sensory factors and consumer preferences. Although high B radiation slightly decreased the sweetness perception and texture likability, it did not influence the other sensory attributes.

Although substituting G radiation for R radiation did not affect macronutrient and micronutrient concentrations in 'Rouxai' lettuce, increasing B radiation increased concentrations of nitrogen, magnesium, sulfur, zinc, and copper. Similarly, substituting 10% G radiation for R radiation did not affect macronutrient and micronutrient concentrations of broccoli (*Brassica oleracea* var. *italica*) microgreens at 5% or 20% B radiation, whereas increasing the B radiation fraction from 5% to 20% at a *PPFD* of 250 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased concentrations of calcium, potassium, and sulfur (Kopsell et al., 2014). In addition, concentrations of macronutrients (phosphorus, potassium, magnesium, calcium, and sulfur) and micronutrients (boron, copper, iron, manganese, molybdenum, sodium, and zinc) in broccoli microgreens were higher under B₄₁ than under B₄₂R₃₀₈ applied for 5 d before harvest (Kopsell and Sams, 2013). This suggests the accumulation of essential macronutrients and micronutrients is primarily mediated by relative B radiation (its fraction of the *PPFD*) rather than absolute B radiation (its *PPFD*). Promotion of nutrient uptake by B radiation is associated with increased stomatal opening, membrane permeability, proton extrusion, and ion transporters (Babourina et al., 2002; Kopsell et al., 2014; Spalding, 2000). Greenhouse-grown lettuce had lower concentrations of potassium, manganese, and molybdenum and higher concentrations of magnesium and copper than lettuce grown under sole-source lighting. These differences could be attributed to different DLIs. For example, increasing the *PPFD* from 105 to 315 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ decreased concentrations of some macronutrients and micronutrients in some *Brassica* species and ornamental crops, but not others (Craver et al., 2018; Gerovac et al., 2016). Reduced nutrient concentrations under high light could be attributed to the dilution of nutrients at high shoot dry mass (Craver et al., 2018). However, greenhouse-grown lettuce in our study had both low concentrations of certain nutrients and low shoot dry mass; therefore, it had a low total content of those nutrients, which was possibly influenced by other environmental variables.

In conclusion, growth, morphology, and coloration of red-leaf lettuce were primarily influenced by B radiation with or without G radiation. Increasing the B *PPFD* decreased shoot mass and leaf expansion but increased the red foliage coloration and concentrations of several macronutrients and micronutrients. Therefore, low B radiation promotes vegetative growth, whereas moderate-to-high B radiation enhances coloration and nutritional value. Temporally changing the spectrum can potentially optimize both yields and coloration. For example, a spectrum with a low ratio of B to R radiation could maximize yields during production, whereas a subsequent spectrum with a high ratio of B to R radiation 1 week before harvest could enhance red foliage coloration (Owen and Lopez, 2015). Interestingly, the role of G radiation in growth regulation depended on the B *PPFD*. Although substituting G radiation

for R radiation generally did not influence lettuce growth under little or no B radiation, it decreased the yield under moderate or high B radiation. Sensory attributes and consumer preferences were generally unaffected by the quality of sole-source lighting but unfavorable for greenhouse-grown plants.

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