Blue Wavelengths from LED Lighting Increase Nutritionally Important Metabolites in Specialty Crops

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Abstract. Light is one of the most important environmental stimuli impacting plant growth and development. Plants have evolved specialized pigment-protein complexes, commonly referred to as photoreceptors, to capture light energy to drive photosynthetic processes, as well as to respond to changes in light quality and quantity. Blue light can act as a powerful environmental signal regulating phototropisms, suppression of stem elongation, chloroplast movements, stomatal regulation, and cell membrane transport activity. An emerging application of light-emitting diode (LED) technology is for horticultural plant production in controlled environments. Work by our research group is measuring important plant responses to different wavelengths of light from LEDs. We have demonstrated positive impacts of blue wavelengths on primary and secondary metabolism in microgreen and baby leafy green brassica crops. Results show significant increases in shoot tissue pigments, glucosinolates, and essential mineral elements following exposure to higher percentages of blue wavelengths from LED lighting. The perception of energy-rich blue light by specialized plant photoreceptors appears to trigger a cascade of metabolic responses, which is supported by current research showing stimulation of primary and secondary metabolite biosynthesis following exposure to blue wavelengths. Management of the light environment may be a viable means to improve concentrations of nutritionally important primary and secondary metabolites in specialty vegetable crops.

Illumination is a powerful environmental stimulus impacting a wide range of plant metabolic processes. Plant species have evolved photoreceptors to sense the light environment and adjust to changing environmental conditions through modulation of cellular processes (Smith, 1982). Unique plant photoreceptors respond to changing light quality and quantity through developmental and physiological responses commonly referred to as photomorphogenesis (Christie, 2007). Photosynthetically active radiation is energy associated with wavelengths of visible light (400–700 nm) predominantly absorbed by leaf tissues. Photochemistry in plants is initiated by absorbed quanta, which differ in quantum energy level and absorption capacity of photosynthetically active pigments based on wavelength (McCree, 1973). Thus, the spectral distribution of light sources in plant production will determine photomorphogenic responses. LEDs now provide the option of selecting

specific wavelengths to complement photoreceptor pigments for targeted plant physiological responses (Massa et al., 2008; Morrow, 2008).

Maximum light absorption by chlorophyll pigments and quantum yield of photosynthesis occur primarily in the blue and red regions of the visible light spectrum (McCree, 1972). Plants have evolved other specialized photoreceptors to regulate responses to these physiologically important wavelengths. Phytochromes are primarily red-light photoreceptors and distinguish between red and far red wavelengths to control physiological responses such as seed germination and flowering (Chaves et al., 2011; Fraikin et al., 2013; Vierstra and Zhang, 2011). Cryptochromes, phototropins, and F-box proteins (a specific structural motif associated with signal transduction and regulation of the cell cycle) are blue-light receptors responding to blue/ultraviolet (UV) light wavelengths. Cryptochromes trigger signaling molecules that regulate responses such as circadian rhythms and stem elongation, whereas phototropins control chloroplastic movements to maximize absorption of light (Briggs and Christie, 2002; Christie, 2007). UVR8 is a recently identified UV-B light photoreceptor believed to initiate regulatory changes in gene expression involved in UV-acclimation of plants in sunlight conditions (Fraikin et al., 2013). The mechanisms of light reception include conformational changes in the receptor chromophore molecule upon photoisomerization to initiate chromophore-protein interactions, which transform light signals into biological signals capable of regulating light-inducible gene expression (Fraikin et al., 2013).

Plant responses to blue-light stimuli include phototropisms, suppression of stem elongation, chloroplast movements, stomatal

regulation, and genetic expression (Baum et al., 1999). Phototropins (phot 1 and phot 2) are plasma membrane-bound serine/threonine kinases that act as blue-light-activated regulators, which optimize photosynthesis and plant growth in low-light environments and can also reduce risk of photodamage (Christie, 2007; Fraikin et al., 2013). The xanthophyll cycle pigments (zeaxanthin, antheraxanthin, violaxanthin) in plants are vital for energy dissipation of excess absorbed radiant light energy. Under high-light stress, violaxanthin is rapidly and reversibly de-epoxidized into zeaxanthin via the intermediate antheraxanthin (Demmig-Adams and Adams, 1996). The chemical transformation of violaxanthin to zeaxanthin is required for the conversion of photosystem II (PSII) from a state of efficient light harvesting to a state of high thermal energy dissipation, which is usually measured as a nonphotochemical quenching of chlorophyll fluorescence (Havaux et al., 2007). Zeaxanthin can modulate blue-light-dependent responses in plants and is believed to be an important photoreceptor for blue-light-activated plant responses (Briggs and Huala, 1999; Kopsell et al., 2014; Tlałka et al., 1999).

Convincing scientific evidence now supports the association between dietary choices and chronic disease expression. The cornerstone of recommended dietary guidelines is increased consumption of fruit and vegetable crops, which provide human diets with many essential vitamins and minerals important for health maintenance. Vegetables also contain secondary metabolite phytochemicals, which provide benefits beyond normal health maintenance and nutrition and play active roles in chronic disease reductions (Kopsell and Kopsell, 2010). Stress is a term used to collectively describe numerous conditions

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that can have negative impacts on plant performance, such as drought, pathogen attack, drastic changes in temperature, high- or low-light conditions, and/or mineral nutrient imbalances. The production of antioxidant compounds within plants can increase or decrease in response to various forms of abiotic environmental stress (Kopsell et al., 2007, 2011). Capacities such as wavelength control, high light output, and low radiant heat emissions are making LEDs a popular alternative to traditional gas-filled or incandescent filament lamps in controlled environment plant production (Martineau et al., 2012; Massa et al., 2008; Morrow, 2008). Work in our program has been focused on identifying physiological plant responses to changing light quality and light quantity using LEDs. Of particular interest is the ability to modulate concentrations of nutritionally important secondary metabolites with applications of blue-light wavelengths.

IMPACTS OF BLUE LIGHT ON THE ACCUMULATION OF NUTRITIONALLY IMPORTANT PIGMENTS

Photochemical reactions of photosynthesis occur in the thylakoids when light energy is captured by chlorophyll and carotenoid pigments and converted into chemical energy. Within the thylakoid membranes of chloroplasts, carotenoids are in close association with specific protein complexes of PSI and PSII and function to help harvest light energy during photosynthesis and dissipate excess energy before photodamage occurs (Demmig-Adams and Adams, 1996; Kopsell et al., 2012). Biological activities attributed to chlorophyll derivatives consistent with cancer prevention include interference with oral absorption of carcinogens, antioxidant and antimutagenic activity, mutagen trapping, modulation of xenobiotic metabolism, and induction of apoptosis (Ferruzzi and Blakeslee, 2007; McQuistan et al., 2012). Chlorophyll *a* and *b* concentrations in kale (*Brassica oleracea* var. *acephala*) seedlings were highest when exposed to the narrow-band LED wavelengths of 640 and 440 nm, establishing a positive correlation between wavelength and chlorophyll accumulation in brassica seedlings (Lefsrud et al., 2008). Kopsell et al. (2014) demonstrated dramatic increases in chlorophyll pigment concentrations in sprouting broccoli (*B. oleracea* var. *italica*) microgreens grown under LED light when compared with fluorescent/incandescent lamps in controlled environments. In their study, the highest concentrations of chlorophyll pigments were found under 20% blue (470 nm)/80% red (627 nm) at an intensity of $250 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. However, Kopsell and Sams (2013) reported no impact on chlorophyll pigment concentrations in sprouting broccoli microgreens when the light environment was changed from 12% blue (470 nm)/88% red (627 nm) at $350 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 100% blue at $41 \pm 2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for a 5-d period before harvest,

which may indicate blue light intensity is a determining factor in photochemical responses. Lin et al. (2013) measured no difference in chlorophyll pigment concentrations in mature lettuce (*Lactuca sativa* var. *capitata*) among red/blue, red/blue/white, and fluorescent lamp treatments at $210 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Li and Kubota (2009) supplemented cool white fluorescent light with different LED wavelengths to determine impacts of supplementation on phytochemical contents in 'Red Cross' baby leaf lettuce. These authors showed no impacts on chlorophyll concentrations in baby lettuce when fluorescent light treatments containing 23% blue (400–500 nm)/52% green (500–600 nm)/24% red (600–700 nm) at $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ were compared with fluorescent light supplemented with blue LED light to achieve 55% blue/31% green/13% red at the same intensity. In a recent study, chlorophyll pigments in 30-d old Chinese kale (*B. oleracea* var. *alboglabra*) did not differ among the LED light treatments of 10% blue (470 nm)/90% red (627 nm), 20% blue/80% red, and 40% blue/60% red, but were significantly higher than kale grown under fluorescent/incandescent light at similar light intensities of $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Kopsell et al., unpublished data). Chlorophyll *a* and *b* pigments in leaf tissue maximize light absorption at 663 and 642 nm, respectively, and at 430 and 453 nm, respectively (Lefsrud et al., 2008). Data may show leafy specialty crops produce higher concentrations of chlorophyll pigments in response to higher intensities of blue wavelengths in the light environment; however, responses may differ based on plant ontogeny and species genetics.

Carotenoids function to help harvest light energy, mostly in the blue-green wavelength range, which is transferred to the photosynthetic reaction centers. The conjugated double-bond systems of the carotenoids create light-absorbing chromophores, which result in the distinctive colors associated with carotenoid plant pigments (Cunningham and Gantt, 1998). Kopsell et al. (2014) demonstrated dramatic impacts on carotenoid pigment concentrations in sprouting broccoli microgreens grown under LED light when compared with fluorescent/incandescent lamps in controlled environments. In their study, the highest concentrations of β -carotene and lutein were found under the 20% blue (470 nm)/80% red (627 nm) light treatment, the highest concentrations of antheraxanthin and total integrated carotenoid pigments were found under the 20% blue/70% red/10% green (530 nm) light treatment, and the highest concentrations of neoxanthin and violaxanthin were found under the fluorescent/incandescent light treatment, with all treatments at the same intensity of $250 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Neoxanthin is enzymatically converted from violaxanthin within the carotenoid biosynthetic pathway in plants. *Cis*-isomers of both violaxanthin and neoxanthin are cleaved to form xanthoxin, a precursor to the important plant regulatory hormone abscisic acid (Nambara and Marion-Poll, 2005). Neoxanthin, a major carotenoid in

green leafy vegetables, is reported to induce apoptosis in human prostate cancer cells in vitro (Asai et al., 2004). Li and Kubota (2009) showed that white light supplemented with blue light (476 nm) to produce $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ resulted in significantly higher lettuce leaf tissue β -carotene and total xanthophyll carotenoids when compared with the white light control or white light supplemented with green light only (526 nm). Lin et al. (2013) reported no differences in total carotenoid concentrations in lettuce among red (660 nm)/blue (454 nm) LEDs, red/blue/white LEDs, or fluorescent light treatments at high photon flux ($210 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Moreover, Martineau et al. (2012) reported no differences in β -carotene, lutein, or neoxanthin in lettuce grown under natural light, natural light supplemented with high-pressure sodium lamps, or natural light supplemented with red (640 nm)/blue (450 nm)/white LEDs, with all light treatments at $\approx 190 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

At low photon flux ($50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for 10 d of exposure, carotenoid concentrations in buckwheat (*Fagopyrum tataricum*) sprouts were highest under white LEDs and did not differ when exposed to blue (470 nm) or red (660 nm) LED light (Tuan et al., 2013). Kopsell and Sams (2013) reported significantly higher shoot tissue β -carotene, violaxanthin, and total xanthophyll cycle pigments in sprouting broccoli microgreens when the light environment was changed from 12% blue (470 nm)/88% red (627 nm) at $350 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 100% blue at $41 \pm 2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for a 5-d period before harvest. Additionally, Gangadhar et al. (2012) showed that total carotenoid pigment concentrations in leaf tissues of chili pepper (*Capsicum annuum*) seedlings were higher under LED lighting treatments than for fluorescent light at low photon flux ($70 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Results from the study also showed that blue (460 nm) LEDs resulted in significantly higher leaf tissue carotenoids in the pepper leaves as compared with only red (660 nm) or red/blue (1:1 ratio). Similar to chlorophyll pigments, concentrations of individual and total carotenoid pigments appear to be influenced by blue wavelengths in the light environment and also by plant ontogeny and species genetics.

IMPACTS OF BLUE LIGHT ON THE ACCUMULATION OF NUTRITIONALLY IMPORTANT GLUCOSINOLATES

Glucosinolates are sulfur-containing secondary metabolites present in brassica species (Stoewsand, 1995). Glucosinolates have no identifiable primary function in plants, but are theorized to protect against predation and pathogens, as well as to act as sulfur storage reserves (Zukalová et al., 2002). Following cellular disruption, glucosinolates are enzymatically decomposed by the enzyme myrosinase and produce mixtures of volatile and nonvolatile compounds including isothiocyanates, thiocyanates, and nitriles possessing anticarcinogenic properties (Fahey et al.,

1997; Heaney and Fenwick, 1980; Stoewsand, 1995).

Previous research has demonstrated that the light environment can impact glucosinolate concentrations in specialty crops (Charron and Sams, 2004; Kopsell and Sams, 2013; Lefsrud et al., 2008). Kopsell et al. (2014) showed the potential to manipulate glucosinolate concentrations through changes in light quality. In that study, LED light treatments of 5% blue (470 nm)/95% red (630 nm), 5% blue/85% red/10% green (530 nm), and 20% blue/80% red at an intensity of $250 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ cause significantly higher individual and total aliphatic and total indole glucosinolates than broccoli microgreens grown under the fluorescent/incandescent light treatment. Kopsell and Sams (2013) reported significantly higher shoot tissue total aliphatic and aromatic glucosinolates in sprouting broccoli microgreens when the light environment was changed from 12% blue (470 nm)/88% red (627 nm) at $350 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 100% blue at $41 \pm 2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for a 5-d period before harvest. In that study, the short-duration blue-light treatment before harvest significantly increased individual glucosinolates of epiprogoitrin, glucoraphanin, and gluconasturtiin in sprouting broccoli microgreens. Lefsrud et al. (2008) found higher sinigrin (an aliphatic glucosinolate) concentrations in kale grown under LEDs at individual wavelengths of 730 nm ($15.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and 640 nm ($253.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), but could not detect sinigrin in the kale tissues following a 7-d exposure to 440 nm ($10.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). An earlier study showed that blue, green, and white colored mulches reflected 25%, 7%, and 41% of incoming solar radiation, respectively, in the blue ($450 \pm 5 \text{ nm}$) wavelengths impacted glucosinolates in the root crop turnip (*Brassica rapa* var. *rapa*). Total glucosinolate concentrations in turnip were significantly higher for plants receiving higher percentages of reflected blue light from blue colored mulches (Antonious et al., 1996). Glucosinolates classes are divided based on amino acids side chain derivatives. Aliphatic glucosinolates are derived from Ala, Leu, Ile, Val, and Met, aromatic glucosinolates are derived from Phe or Tyr, and indole glucosinolates are derived from Trp (Sønderby et al., 2010). It is possible that glucosinolates side chain elongation and modifications through amino acid metabolism are impacted by narrow-band wavelengths. Blue wavelengths in the light environment can influence glucosinolate concentrations, with the impacts affected by intensity of blue light, plant ontogeny, and species genetics.

IMPACTS OF BLUE LIGHT ON THE ACCUMULATION OF NUTRITIONALLY IMPORTANT MINERAL ELEMENTS

The blue light receptor phototropins (phot 1 and phot 2) regulate hypocotyl phototropisms in a fluence-dependent manner, with phot 1 functioning at both low ($0.01\text{--}1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)

and high ($>1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) fluence rates and phot 2 functioning at only high fluence rates (Inada et al., 2004; Sakai et al., 2001; Zhao et al., 2013). The phototropins confer their effects through changes in Ca^{2+} ion homeostasis (Zhao et al., 2013) and mobilize Ca^{2+} in response to blue light. Under low blue light, phot 1 controls the flux of Ca^{2+} through plasma membrane channels; whereas, under high blue light, phot 2 causes increases in cytosolic Ca^{2+} through release from internal stores and through plasma membrane channels (Harada and Shimazaki, 2007). Blue light exposure can also cause significant changes in guard cell membrane transport activity through variations in K^{+} and H^{+} fluxes and corresponding impacts on pH conditions (Babourina et al., 2002). Even though Ca^{2+} acts as an important secondary messenger crucial for cellular responses to environmental stimuli, the ability of blue light to influence mineral element movements through phototropin functioning is probable.

Kopsell and Sams (2013) reported significantly higher shoot tissue concentrations of P, K, Mg, Ca, S, B, Cu, Fe, Mn, Mo, Na, and Zn in sprouting broccoli microgreens when the light environment was changed from 12% blue (470 nm)/88% red (627 nm) at $350 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 100% blue at $41 \pm 2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for a 5-d period before harvest. Further, Kopsell et al. (2014) showed significantly higher concentrations of tissue Ca, K, Mg, P, S, B, Cu, Fe, Mn, Mo, and Zn in broccoli microgreens grown under the higher blue LED light treatments of 20% blue (470 nm)/80% red (630 nm) and 20% blue/70% red/10% green (530 nm) at an intensity of $250 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, when compared with a fluorescent/incandescent light treatment at the same intensity. The impacts of blue light on stomatal opening and membrane transport activity may be the underlying cause for such increases in macronutrient and micronutrient accumulations in the broccoli microgreen tissues, but exact mechanisms remain unclear (Kopsell et al., 2014; Kopsell and Sams, 2013).

Specialized plant photoreceptors sense and react to changing light quality and quantity through developmental and physiological responses. Light interception causes photoisomerization of chromophore complexes, which ultimately leads to gene regulation of specific biochemical pathways. Phototropin blue-light receptors control such plant responses as phototropisms, suppression of stem elongation, chloroplast movements, and stomatal regulation. Downstream regulation from blue-light stimuli may also include metabolite fluxes in nutritionally important plant secondary metabolic pathways. Research into the photomorphological impacts of blue wavelengths using LEDs has shown responses to be determined, in part, by photon flux intensity, photoperiod, plant ontogeny, and species genetics. With all of these interacting factors, much more information is needed before producers can successfully manage specific wavelengths in the light environment to maximize the nutritional functionality of specialty vegetable crops.

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